A fish fit for Ozymandias? : The ecology, growth and osteology of *Leedsichthys* (Pachycormidae, Actinopterygii).

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Abstract

In this thesis, I describe work to resolve issues of bone identifications that have been outstanding since Smith Woodward's initial description in 1889, to assess the taxonomic validity of material assigned to the hypodigm of *Leedsichthys* and the interrelationships of the members of Family Pachycormidae. In addition I look at the palaeoecology of this animal on the basis of its size and growth and its locomotion capabilities and its likely feeding abilities and behaviour.

Chapter 2 includes a review of the history of work on *Leedsichthys*, with particular reference to the discoveries made in the Peterborough district, here questions over the type material are raised. In chapter 3, archival photographs and papers are used to establish the distinction between the type material, the tail specimen, and the gill basket specimen. In chapter 4, occurrences of *Leedsichthys* outwith the Peterborough district are considered, including the announcement of a new locality extending the range of the taxon into the Kimmeridgian. Some identifications of previously misidentified bones are made, specifically the hypobranchial and dorsal fin-rays. Feeding trace fossils are interpreted in the context of *Leedsichthys*. In chapter 5, a new Callovian pachycormid is described from the Oxford Clay of Peterborough district, and used in a reworking of Lambers' 1992 phylogenetic analysis of the interrelationships of the Pachycormidae. The Pachycormiformes are redefined on the basis of derived characters. In chapter 6, the value of gill rakers as a source of taxonomic characters is considered, with specific reference to their use in Lambers' 1992 character set, and the validity of *Leedsichthys notocetes* as a distinct species. Characters are revised and interrelationships among the Pachycormiformes reassessed using additional characters to supplement a revised version of Lambers' original character set. In chapter 7, specimens are analysed using growth marks and scaling, in order to establish estimates of length-at-age for *Leedsichthys*. In chapter 8, the bone identifications of Smith Woodward (1889b) are revised, and further bone morphologies identified from within the hypodigm of the genus. In chapter 9, the size estimates derived in chapter 7 are used to inform interpretation of *Leedsichthys* palaeoecology, focussing primarily on locomotion and feeding. In the conclusions, an up-to-date reconstruction is presented.

Throughout the thesis (with the exception of chapter 5, the type description), *Martillichthys* is referred to as 'Taxon 13'.

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NOÈ, L.F. LISTON, J.J. AND EVANS, M. 2003. The first relatively complete exoccipital-opisthotic from the braincase of the Callovian pliosaur, *Liopleurodon*. *Geological Magazine* 140: 479-486.

Preface

OZYMANDIAS OF EGYPT

I met a traveller from an antique land
Who said: "Two vast and trunkless legs of stone
Stand in the desert. Near them on the sand,
Half sunk, a shattered visage lies, whose frown
And wrinkled lip and sneer of cold command
Tell that its sculptor well those passions read
Which yet survive, stamped on these lifeless things,
The hand that mocked them and the heart that fed.
And on the pedestal these words appear:
'My name is Ozymandias, King of Kings:
Look on my works, ye mighty, and despair!'
Nothing beside remains. Round the decay
Of that colossal wreck, boundless and bare,
The lone and level sands stretch far away.

Percy Bysshe Shelley, 1818

Prefatory Remarks

Leedsichthys was a problem that I found in a drawer eight years ago. Well, a lot of drawers, actually. I was curating the six hundred odd specimens of the Hunterian Museum's Alfred Leeds' collection of vertebrate fossils from the Oxford Clay around Peterborough, and had intended to identify every single element of every specimen as I added it to the Hunterian's computer catalogue. For most specimens, of course, there was Andrews' landmark pair of catalogues, replete with images and descriptions of the detailed osteology of the marine reptiles in the collections of both the Natural History Museum (London) and the Hunterian Museum. It was a great way to expand my anatomical knowledge, which I had originally acquired at medical school in Edinburgh, then added to with later dinosaurian work. The marine reptiles were a welcome extension. But there was no equivalent reference for *Leedsichthys*. No images of any bones in the literature at all, beyond two fragmentary gill rakers, and a picture of the tail.

I was quite baffled by this. The animal had been described with great uncertainty in 1889, was clearly large and of significant palaeoecological importance, and yet had been

studiously ignored by everyone (except for David Martill) for the ensuing century, so that there was still a void when it came to identification of the bones of *Leedsichthys*, never mind interpret its lifestyle. It was as though it was too large for palaeoichthyologists to work on, and too ichthyological for other vertebrate palaeontologists to study.

I did some research, uncovering (somewhat staggeringly) that the Hunterian Museum's specimen, by virtue of the sheer volume of bone, was the most extensive and complete specimen known, with more than twice the mass of bone of the holotype material (BMNH P.6921) (fig. 2.8). At the time, I was looking for a vertebrate palaeontology postgraduate research project – and the most complete specimen of the biggest fossil fish enigma of the Mesozoic was sitting forgotten in a cabinet in my own museum.

So that's how I first encountered the problem – way before the Star Pit specimen ('Ariston') came to light in July 2001, and that had to suddenly be dealt with and incorporated in some way into the project.

I have to confess, I was drawn to working on this animal through my disbelief that there was no 'guide' for identification of its remains. Smith Woodward's cautious verbal description featured no figures whatsoever, and I would like to think that this work has at least achieved some progress on that.

There was a huge amount of 'ground work' that needed to be completed before the project really started. Smith Woodward's failure to return to the task of description of the bones has led to generations of curatorial staff ignoring *Leedsichthys* material. This is also partly due to the research community's failure to engage with the challenge that working with this animal's remains represents, as specimens that are periodically examined by researchers are less likely to have their provenance or documentation misplaced over time. As such, a substantial part of this project's ground work involved retrospectively curating a large quantity of material that had been neglected, to various degrees, by a range of institutions. Archival research was required to locate documentation that can shed limited - but urgently needed - light on the provenance of the material. The fossilised material itself is delicate, subject to pyrite damage in poor storage (a common problem of twentieth century storage of Oxford Clay material), is unidentified (and regarded as unidentifiable), and it is often too large for regular storage, so is placed in 'irregular' storage – frequently on the tops of cabinets. This has on occasion led to further problems with separation of parts of specimens from their documentation.

One of the consequences of this, is that I have occasionally had to make judgements on the relatedness of elements that are often stored far apart from each other, for which there is reason to believe that there is a relationship, although the necessary documentation that would confirm this cannot always be located.

Another problem is the degradation of the specimens through time, which has necessitated the investment of a substantial quantity of time in reassembling the bones, in order to ascertain something of the shapes of the bones. Once a bone is reassembled, it is an ongoing process to maintain its integrity. You examine a reassembled bone in the full knowledge that doing so will almost certainly cause it to break. In a funded study, casts would have been made from bones to deal with their articulations, in order to reduce handling and subsequent damage. This combination of large and difficult to manipulate bones (on the scale of a sauropod dinosaur, in some cases), the preservation of limited discrete portions of its skeleton (Aldridge 1986) and extreme fragility, has served to deter researchers since Smith Woodward, in spite of the intrinsic attraction of an animal (if size is any measure of success, Peters 1983) that was clearly very successful in a rich ecosystem, and therefore worthy of attention. Carl G. Jung, who dreamed of being a palaeontologist before ending up in Medicine (Jung 1960, ref Additional MS. 81277 B) once observed that the symbol 'ichthys' for the fish; 'It is unlikely that 'Ιχθυζ is simply an anagrammatic abbreviation of 'Ι[ησουζ] Χ[ριστοζ] Θ[εου] Υ[ιοζ] Σ[ωτηρ], but rather the symbolical designation for something far more complex...the best possible way of describing and formulating an object that is not completely knowable" (Montgomery 1974) and this perhaps (in terms of preservation) reflects part of the reason why *Leedsichthys* has not been worked on. The lack of identified elements in collections has led to a misperception of a restricted range of bones and a limited range of bones. This led to Lambers (1992) only coding two out of sixteen characters for it in his dataset for Family Pachycormidae, and Mainwaring (1978) excluding it entirely from her analysis of that family. Although many elements of its skeleton do not seem to preserve (due to a presumed reduced ossification of the skeleton), there are a substantial number of different elements that can be distinguished and identified.

When I started this project, Leslie Noè was finishing his PhD on pliosaurs from the Oxford Clay. Both of us were uncovering 'lost' archival material on Alfred Leeds and his collection, and pooling our knowledge of these resources. This meant that he alerted me to the existence of the 1898 letter from Alfred Leeds regarding the discovery of the tail

specimen (BMNH P.10000) that forms the basis of chapter three, and when I discovered a bone that turned out be a pliosaur exoccipital-opisthotic misidentified as a bone of *Leedsichthys* (presumably a vertebra), I gave it to him to describe. The first joint-authored paper forms chapter three, and the second (as only peripherally relevant to *Leedsichthys*) is attached as an appendix (VIII).

So, in between the outreach COPUS exhibition work displaying the fish 'in full' in a museum for the first time anywhere in the world, and leading the longest British palaeo field dig, its been full of challenges, challenges that simply would not have been met without the support of the colleagues and friends that I've encountered – and that is particularly true for an unfunded project.

The fragments that I started with all those years ago, may well have been like the statue of Rameses II that inspired Shelley's poem – hinting at some past glory, with no real trace still surviving to measure it by – but I hope that if we do not have the flesh on the bones now, maybe at least we have some bones to put some of the flesh on.

11/7/2006

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(when I had my crowbar, she had my back). John Wagner and Carlos Ezquerra are thanked for coming up with the 'Big Meg'.

Appreciation is shown to the examination committee of Mike Benton, Peter Meadows and Douglas Neil. The Palaeontological Association, NERC's emergency funding route, the Aggregate Levy's Sustainability Fund, English Nature, the Stamford Geological Society, the East Midlands Geological Society, and the Friends of Peterborough Museum all financially supported over 3,000 hours of the excavation of the *Leedsichthys* specimen 'Ariston', which is gratefully appreciated. Kay Hawkins in particular is warmly thanked for finding the intact skull roof of *Leedsichthys* for me. The Blodwen Lloyd Binns Bequest Fund of the Glasgow Natural History Society paid for the transportation of the transit van filled with Big Dead Fish to Glasgow for study, and also paid for a collections tour through German museums. Financial support critically came from Alf Hatton and Ewen Smith in order to start the project. My measureless thanks go to both Lesley Richmond and Ewen Smith, to Lesley for coercing me into asking for time off to write up, and Ewen for saying 'yes' when he didn't have to: he was there for me at the start and the finish – in other words, when it mattered most. And finally, at the very end, my humble and grateful thanks to Linda and the 'Archies' Angels' team at the Glasgow University Print Unit – printing a thesis in 20 minutes just before the end of a 7 year deadline is no mean kindness....especially on an early closing day.....

Author's declaration

Statement of originality: The work herein contained is entirely my own, the only exception being chapter 3, which was jointly written with L. F. Noè of the Sedgwick Museum, Cambridge, as we had independently found different archival components that went together to form the whole of that investigation. Chapter 2 was published as a chapter in the Mesozoic Fishes 3 volume. Chapter 3 was published in Archives of Natural History. Chapter 4 has been accepted for publication in the journal Oryctos (pending image modifications). Chapter 5 has been accepted for publication in the Mesozoic Fishes 4 volume (pending image modifications). Chapter 6 has been submitted reformatted for Journal of Systematic Palaeontology. Chapter 7 has been submitted reformatted for the journal Palaeontology. Chapters 8 and 9 have not been submitted for publication, but Appendix VII ("From Glasgow to the Star Pit and Stuttgart: A Short Journey Around The World's Longest Fish") is in press for the journal The Glasgow Naturalist.

Definitions

INSTITUTIONAL ABBREVIATIONS

BMNH = Natural History Museum (London), England.

BSPG = Bayerische Staatssammlung für Paläontologie und Geologie, München, Germany.

CAMSM = Sedgwick Museum of Geology, University of Cambridge, England.

G = Dolf Gielen Collection, Paris, France.

GLAHM = Hunterian Museum, The University of Glasgow, Scotland.

I = Museo de Arqueologia, Antofagasta, Chile.

L = Leich Collection, Bochum, Germany.

LEICT = Museum and Art Gallery Leicester, Leicestershire, England.

LEIUG = Leicester University Geology Department, Leicester, England.

NMW = National Museums and Galleries of Wales, Cardiff, Wales.

OUMNH = Oxford University Museum of Natural History, Oxfordshire, England.

PETMG = Peterborough Museum and Art Gallery, Cambridgeshire, England.

PHBW = Privatsammlung Harry Breitkreutz, Enger, Germany.

PMM = Privatsammlung Matthias Metz, Bünde, Germany.

SMNK = Staatliche Museum für Naturkunde Karlsruhe, Germany.

SMNS = Staatliches Museum für Naturkunde, Stuttgart, Germany.

WMfN = Westphalisches Museum für Naturkunde, Münster, Germany.

ANATOMICAL ABBREVIATIONS

afr, anal fin-rays

ang, angular

ao, antorbital

ar, articular

bb, basibranchial

cb1-5, ceratobranchials 1-5

cb5, fused fifth ceratobranchial

cbl1-3, left ceratobranchials 1-3

cbl4, left fourth ceratobranchial

cbr1-3, right ceratobranchials 1-3

cbr4, right fourth ceratobranchial

cfr, caudal fin-rays

cha, anterior ceratohyal

chl, fragments of left ceratohyal overlying matrix around branchial elements

chp, posterior ceratohyal

chr, area where right ceratohyal has been displaced through the skull roof

d, dentary

dfr, dorsal fin-rays

dpt, dermopterotic

dsp, dermosphenotic

dptu, inferior surface of dermopterotic

eb1-4, left epibranchials 1-4

eb1-4op, right epibranchials overlain by right opercle

ecp, ectopterygoid

ex, exoccipital

fm, foramen magnum

g, gular

gr, gill raker

gur, ventral gular ridge

hbl, left first and second hypobranchials

hbl1, left first hypobranchial

hbl2, left second hypobranchial

hbr2, right second hypobranchial

hh, hypohyal

iop, interopercle

lh, left hypohyal

mpt, metapterygoid

mx, maxilla

n, nasal

op, opercle

opu, inner surface of left opercle

p, parietal

par, prearticular

pas, parasphenoid

pfr, pectoral fin-rays

pop, preopercle

pp, postparietal

q, quadrate

rde, rostrodermethmoid

rh, right hypohyal

sag, supraangular

so, supraorbitals

sop, subopercle

sym, symplectic

t, tooth

?eb, possible epibranchial element or fragment of preopercle

?h, possible fragment of hyomandibula

?PU, possible first preural vertebra.

Chapter 1

THE LOVE SONG OF J. ALFRED PRUFROCK

Let us go then, you and I,
When the evening is spread out against the sky,
Like a patient etherized upon a table;
Let us go, through certain half-deserted streets,
The muttering retreats

Of restless nights in one-night cheap hotels
And sawdust restaurants with oyster-shells:
Streets that follow like a tedious argument
Of insidious intent
To lead you to an overwhelming question ...
*Oh, do not ask, "**[How big was]** it?"*

Let us go and make our visit.

(with apologies to) Thomas Stearns Eliot, 1915

Chapter 1

Historical Background To Fossil Vertebrates From The Oxford Clay, And An Outline Of Issues Identified For Resolution At The Start Of The Project.

1.1 - INTRODUCTION

The Oxford Clay is first recorded as a source of fossil vertebrates by Owen (1842), although the one geographical location that he specifically referred to in this context was Honfleur (France). Owen only drew attention to the occurrence of pliosaur material, and it fell to Porter (1861) to explicitly note the occurrence of ichthyosaurs, plesiosaurs and steneosaurs in the Oxford Clay around Peterborough.

The collector Alfred Nicholson Leeds is the most distinguished single collector of fossil material from the Oxford Clay. He began acquiring Oxford Clay fossils at a young age, from the pit across the road from his family home of Eyebury, collaborating with his elder brother Charles Edward Leeds. When the time came to decide which career he would pursue in life, Charles chose not to run the family farm, but to go to Oxford University in 1865. This meant that Alfred Leeds was unable to fulfil his own aspiration of studying medicine, for as the sole remaining brother, he had the responsibility for looking after the Leeds' family's farm (Leeds 1956).

This gave Alfred the opportunity to indulge in what would become a passion for the local fossils. Over more than fifty years he collected over a thousand fossil marine reptiles from the Oxford Clay being so industrially stripped from the area by the brick-making industry (Hillier 1981). Apart from smaller packages (often sold via the dealer Bernhard Stürtz of Bonn to museums throughout Europe), there were two bulk (i.e. consisting of hundreds of specimens) sales of his collected material. The first was to the British Museum (Natural History) over 1889-1892, and included what Henry Woodward noted as 'head bones of a very huge undescribed fish' as well as other similarly large remains. In 1889, Arthur Smith Woodward of the BM(NH) published a first description of a series of disarticulated bones spread over "12 square yards" and believed to belong to a single individual of a species he named *Leedsichthys problematicus* (the following year, he published a revision of the name, with an illustration of some of the material, proposing **Leedsia problematica** instead, for linguistic reasons. Under ICZN rules, this is not a valid change, and the original binomial stands, ICZN 1999), "in honour of its discoverer". In doing so, Smith Woodward stated his belief that the remains belonged to an acipenseroid fish. By

1895, Smith Woodward had changed his mind on the placement of the animal, referring it instead (because of its bifurcating non-segmented fin-rays) to the Family Pachycormidae. Named after the genus *Pachycormus* (meaning 'thick-bodied'), this Family is closely associated with the first radiation of the teleosts (Arratia 1996). Although the new diagnosis seemed slightly at odds with the earlier identification of 'acipenseroid', the apparent conflict was not addressed by Smith Woodward or any subsequent worker.

1.2 - THE GLASGOW SPECIMEN (GLAHM V3363)

In 1915, as part of a purchase from Alfred Leeds, Professor John Walter Gregory (Head of Geology at the University of Glasgow), acquired a specimen (GLAHM V3363) of this animal for the University's Hunterian Museum (the type having already gone to the BM(NH) as part of the First Collection sale). Little work was done on the specimen over the following 80 years, until a curation project on the University's holdings of the Leeds Collection (an additional 'Second Collection' was acquired by Professor Gregory after Alfred Leeds' death in 1917) in 1998 brought the full extent of the specimen to light. Subsequently identified to be the most complete specimen of this fish yet recovered, it was decided that this individual should form the basis of research work into the taxonomic affinities of *Leedsichthys* (with clarification of any of the possible conflicts previously referred to), its ecological role in the Oxford Clay sea ecosystem, and osteological determination of all components heretofore attributed to this animal.

1.3 - THE TAIL SPECIMEN (BMNH P.10000)

An apparently isolated tail had been on display for many decades in the Fossil Fish Gallery of the British Museum (Natural History), identified as *Leedsichthys problematicus* without apparently having any bony elements in common with the type material. This raised the possibility of there being two distinct large bony fishes in the Oxford Clay sea, and required comparison of the type material (BMNH P.6921, with BMNH P.6922 and BMNH P.6925), with the tail specimen (BMNH P.10000) and the Glasgow specimen (GLAHM V3363). Although fish other than pachycormids and teleosts can be found in the fossil record with a homocercal tail (e.g. *Saurichthys*, Chou & Liu 1957), the form of this tail was very far removed from that which would be possessed by an 'acipenseroid' as described by Arthur Smith Woodward (1889a,b).

All of these issues were comparatively small details in relation to the major problem, which was that this animal was apparently the largest bony fish ever, and yet was still a virtual enigma. The lack of work on the taxon meant that it was as difficult to identify its

remains today, as when it was first described in 1889, given Smith Woodward's retraction of all but two of his bone identifications for *Leedsichthys* (Leeds & Smith Woodward 1897). This situation was in striking contrast to work done on the rest of the vertebrate fauna excavated by Alfred Leeds. This was in spite of the fact that those Oxford Clay marine reptiles required a substantial amount of interpretation, due to a scarcity of living close relatives to compare them with. In contrast a pachycormid, being close to the origin of teleosts, would seem to have a substantial amount of reasonably close living relatives for the purposes of comparative anatomy and physiology, thus require less interpretative work.

Leedsichthys is important as an osteichthyan that grew to Standard Lengths no osteichthyan achieves today, which implies a measure of success (Peters 1983). As such, it is important as a successful member of the Family Pachycormidae that was a part of the initial radiation of the teleosts. It also appears to 'break' Cope's Rule (Peters 1983, Freedman & Noakes 2002), in that although pachycormids continued to the end of the Cretaceous Period, their mean maximum size dropped in the Tithonian to just over 2 metres (*Asthenocormus*), and thereafter they did not exceed a Standard Length of 1 metre. The large size of *Leedsichthys* is also of interest, because its range (Callovian-Kimmeridgian) falls within the 20 million year period (Bathonian-Kimmeridgian) in which a leap in size for the largest known dinosaurs takes place, and would seem to parallel this terrestrial development (Benton 1986).

1.4 - STATEMENT OF THESIS

In this thesis, I describe work to resolve issues of bone identifications that have been outstanding since Smith Woodward's initial description in 1889, to assess the taxonomic validity of material assigned to the hypodigm of *Leedsichthys* and the interrelationships of the members of Family Pachycormidae. In addition I look at the palaeoecology of this animal on the basis of its size, its growth, its locomotion capabilities, its likely feeding abilities and behaviour.

Chapter 2

"The animals which inhabit the sea are much less known to us than those found upon land, and the economy of those we are best acquainted with is much less understood; we are therefore too often obliged to reason from analogy where information fails, which must probably ever continue to be the case, from our unfitness to pursue our researches in the unfathomable waters."

John Hunter, 1787

Chapter 2

An overview of the pachycormiform *Leedsichthys*.

2.1 - ABSTRACT

A historical review of work on the Callovian actinopterygian fish *Leedsichthys* is given, and unresolved issues regarding its type material, taxonomic position and palaeobiology are highlighted. Collections and archival research reveal two previously unrecognised exceptionally complete specimens, which should be critical to the future understanding of this animal.

2.2 - INTRODUCTION

One hundred and fifteen years after some of its bones were first described, the extinct Callovian actinopterygian fish *Leedsichthys* remains extremely poorly understood. Understanding has been hindered by the material collected only being very incomplete (Hudson & Martill 1994), crushed and badly fragmented, and there being no site map record of specimens to indicate the relative dispositions of bones within a site prior to collection. This has led to very few anatomical determinations being made to the bones found, with most of those identifications later retracted.

As essential first steps towards improving understanding of this animal, a comprehensive historical review of all published work on this taxon was undertaken, in conjunction with a survey of all known specimens of *Leedsichthys* held in British collections. The aim of the literature review was to reduce the number of contradictions and inaccuracies persisting in the literature regarding this fish, and the primary purpose of the collection survey was to assess the most complete specimens for future work. In addition, it was hoped that the collection work would identify more limited specimens that represented components not preserved in the more complete individuals, as well as identify and exclude other specimens that might have been passively included within the genus, simply because it seemed to represent 'the large fish from the Oxford Clay', rather than because it contained remains comparable to the type material. This would enable a more refined and rigorous diagnosis of *Leedsichthys* to be produced in the future.

This paper will present a historical review of all published work on the taxon, and present initial results from collections and archival research on historically collected specimens, with the intention of resolving some of the conflicts and inaccuracies in the literature, and to highlight important specimens for future work on this animal.

2.3 - HISTORICAL OVERVIEW

From 1867 to 1917, gentleman farmer Alfred Nicholson Leeds indulged his passion for collecting vertebrate fossils from the Oxford Clay that cropped out near his home at Eyebury, near Peterborough, in Cambridgeshire (then Northamptonshire), England (Leeds 1956). His skill as a fossil collector and preparator, his interest in anatomy, and the occasional help of his elder brother Charles in the early years, enabled him to reassemble a large number of these skeletons, mainly of marine reptiles from the Callovian Oxford Clay sea. By September 1885 the British Museum (Natural History) – now The Natural History Museum (London) – had become aware of his collection, and an arrangement was made for it (known afterwards as "the First Collection") to be purchased in its entirety. Amongst that first collection was a series of bones which Arthur Smith Woodward christened *Leedsichthys problematicus* (Smith Woodward 1889b).

The first time that any of these bones were examined by anyone other than Alfred Leeds, was in May 1886 (Hulke 1887). At this time, Dr. Henry Woodward (Keeper of Geology at the NHM from 1880-1901) apparently agreed with his co-visitor Dr. J. W. Hulke that two large thin flat bony plates appeared to be dermal armour from the stegosaurian dinosaur *Omosaurus* (now *Lexovisaurus*) *durobrivensis*. In 1888, Professor Othniel Charles Marsh, being familiar with "numerous types of Dinosaurian dermal armour" in the United States, visited the collection at Eyebury, and "expressed the opinion that the remains were piscine" (Smith Woodward 1889b). At the start of 1889, Arthur Smith Woodward, also of the NHM, published a paper "On the Palaeontology of Sturgeons" in which he reviewed the geological record of acipenseroid fish (Smith Woodward 1889a). Smith Woodward (1889a: 31) remarked: "There is some reason to hope that before long evidence of other Acipenseroids will also be definitely recognized [sic] in later Jurassic rocks. In the collection of Oxford Clay Vertebrates made by Alfred N. Leeds, Esq., of Eyebury, Peterborough, there are traces of a very large fish, having stiff branched fin-rays and irregular dermal bones; and these fossils are apparently most nearly paralleled by Acipenseroids, though no elements sufficiently like those of known genera have yet been found to render any determination certain."

In September 1889, at the 59th meeting of the British Association for the Advancement of Science, Smith Woodward presented "preliminary notes on some new and little-known British Jurassic fish", within which he described the new genus and species *Leedsichthys problematicus* (Smith Woodward 1889b, 1889c, 1890a). As an associated series of bones he declared that it could "only be provisionally defined" (hence the choice of species

name) (Smith Woodward 1890a: 585) and that "if [the following identifications are] correct, the axial skeleton of the trunk still remains to be discovered." (Smith Woodward 1889b: 452). Smith Woodward's uncertainty is further reflected in his use of "perhaps", "suggestive of", "may be" and "probably"" to preface all of his osteological identifications (which included frontal, angular, hyomandibular, branchial arches, gill rakers, preoperculum or clavicle, branchiostegal rays and fin-rays) (Smith Woodward 1889b: 452-453). Smith Woodward concluded his description by stating that the "characters of the gill-rakers, branchiostegal rays, and pectoral fin-rays, taken together" justified the establishment of a new genus, the gill-rakers of which (he noted) had also been obtained from the Oxford Clay of Vaches Noire in the north of France (p. 454) (fig. 2.1). In a specimen of several hundred parts, none was figured in this description, although a brief three paragraph follow-up paper featured a plate with a figure of the gill rakers (Smith Woodward 1890b). There, Smith Woodward proposed shortening the generic name that he had coined for the fish to *Leedsia*, and conforming the specific name to *problematica* - but this is simply not valid under the rules of the International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature, 1999). All that Smith Woodward (1890b) did was create a *nomen novum*, which would only become active in the unlikely event that the original name *Leedsichthys* became invalid for reasons of homonymy. But this name still proliferated throughout both the scientific literature and museum collections. Smith Woodward (1890b: 292) emphasised that "the systematic position of the fish remained doubtful, owing to the fragmentary character of its skeleton".

What might have led Smith Woodward to conclude an 'acipenseroid' nature for this new fish? At the time that he wrote, Smith Woodward was referring to a group of fossil fishes that consisted only of the Family Chondrosteidae in the Mesozoic (no evidence of Acipenseridae being older than Eocene at that time). This family included the genera *Chondrosteus* (Hettangian-Pliensbachian) and *Gyrosteus* (Toarcian) – both large (growing to over a metre – over six in the latter case), toothless, lacking fully ossified vertebrae, and without scales (except in fulcral form on the tail) (Smith Woodward 1889a). It is also possible that he thought of *Leedsichthys* with its large gill rakers and incompletely ossified axial skeleton as something perhaps related to a large benthic filtering sturgeon. *Leedsichthys* would certainly appear to conform to this basic set of characteristics.

But Smith Woodward had changed his mind regarding the animal's taxonomic position by the time he came to publish the third part of the Catalogue of the Fossil Fishes in the British Museum (Natural History) in 1895: at the end of the section on the Family

Pachycormidae, he concludes "to the Pachycormidae may also perhaps be referred the large problematical fish from the Oxford Clay of Peterborough named Leedsia problematica... The type specimens from the Leeds Collection are now preserved in the Museum, but the determination of all the bones except the gill-rakers (? Or gill-supports) is still so uncertain, that it seems advisable to postpone the description of them until the final Supplement, when more satisfactory evidence of their true nature may perhaps be forthcoming. The massive bones, which have been compared with branchiostegal rays, will most likely prove to be vertebral arches." (Smith Woodward 1895). Smith Woodward then noted the occurrence of the genus in Vaches Noire, before citing its presence in the Kimmeridge Clay of Dorset – something of which no trace exists outside of this entry by Smith Woodward, and a similar note made by him some years later when he revised the fish section of the third edition of Zittel's Text-Book of Palaeontology (Zittel 1925). The promised Supplement to the Catalogue never came (it was only partly developed in manuscript form, and no reference to *Leedsichthys* occurs within this document), and no more complete description came from Smith Woodward regarding this animal, as his attention as regards major projects was diverted elsewhere to work on the "Piltdown Man" and the sauropod dinosaur *Cetiosaurus leedsi*.

What made Smith Woodward change his mind regarding the Family to which this fish belonged? It is hard to say – in reviewing the criteria that he sets for inclusion within the Pachycormidae in the "Catalogue", few could really be applied to *Leedsichthys*. Like other fish (including 'acipenseroids'), many pachycormids have incompletely ossified vertebral centra, but many subsequent workers have proposed the mechanism of paedomorphosis as the means by which different branches of acipenseriformes have attained an adult state with limited ossification of areas of their skeleton (e.g. de Beer 1937, Bemis & Grande 1992). Clearly this avenue of developmental change is not exclusively open to this group of fishes, so it should not be seen as a diagnostic characteristic. The presence or absence of most of the characteristics listed by Smith Woodward in the "Catalogue" as diagnosing members of Pachycormidae simply cannot be assessed because of the minimal amount of anatomical analysis done on the specimens, then or since. Only the elongate nature of the pectoral fin, the closely set, articulated, slender and distally dividing fin-rays, the robust cranial/facial bones, or the numerous and closely arranged vertebral arches might be applicable to the specimens that Smith Woodward had at hand. The attribution to Pachycormidae certainly seems a tentative one. This is underlined by his statement some years later that beyond the gill rakers and fin-rays were "... other miscellaneous bones, which have not been identified." (Leeds & Smith Woodward 1897: 191).

In March 1898, Alfred Leeds wrote to Arthur Smith Woodward to inform him of a new find of *Leedsichthys*, which included a tail over 2.5 metres in height. It took Alfred and his family (already very experienced in reconstructing broken bone fragments) some months to assemble the tail for delivery, for its fragile nature meant that it came out of the clay in thousands of pieces, some smaller than a "knitting needle" in diameter (Leeds 1956: 73). Because of the remarkable nature of this specimen, it was accorded a special number in the register of the Natural History Museum's fossil fish – P.10000 (Martill 1986a).

Although lacking haemal arches and hypurals, and consisting only of fin-rays, it was still a remarkable specimen to behold (fig. 2.2). Not published on at the time, it became, through its prominence in the NHM's fish gallery, the most famous single component of the fish. Certainly, the way that the bony rays of the tail branched without segmentation can only have made Smith Woodward feel more confident about his attribution of the fish to the Pachycormidae, and he still placed *Leedsichthys* in that family when he revised the fish section of the third edition of Zittel's Text-Book of Palaeontology (Zittel 1925).

In September 1901, Von Huene visited the Woodwardian (now the Sedgwick) Museum in Cambridge University, and in a report (Huene 1901) on some of the dinosaur material there from the Oxford Clay around Peterborough, he figured some of the elongate and curved *Leedsichthys* bones (fig. 2.3) as caudal spines from the stegosaurid *Omosaurus*. He stated that "...there are about a dozen long, bent spines. Without a doubt, they belong to the tail of a stegosaurid, probably to the English genus *Omosaurus*. According to Marsh, *Stegosaurus* bears several pairs of long spines at the end of its tail. Those from Cambridge are not paired, but apparently are arranged in one row. Some of them fit on top of each other along their bases indicating that they belonged to one individual. The last and smallest piece that has a broad base is strongly bent backwards and branched in two." (Huene 1901: 717-718) This error was noted by Leeds in a letter to Smith Woodward on the 22nd December in the same year (correspondence in the Official Archives of The Natural History Museum, DF100/32/69), and formally recognised in print by Hoffstetter (1957) as belonging to a fish, probably *Leedsichthys*. Galton (1985) later incorrectly assumed that the figure represented the gill rakers of *Leedsichthys*, but they are more likely to be dorsal fin spines.

Specimens continued to emerge from the Oxford Clay over the following years, and a variety of institutions acquired specimens of *Leedsichthys* from A. Leeds (often via the dealer Stürtz of Bonn, a personal friend of A. Leeds) and other collectors (Leeds 1956). Of

particular note was a remarkably intact gill basket (BMNH P.10156) with ceratohyal and hyomandibula (fig. 2.4) (Martill 1988), which was bought from A. Leeds by the NHM in July 1905. In January 1915, the Hunterian Museum (University of Glasgow) purchased two specimens from A. Leeds for its collection (Liston 1999) (GLAHM V3362 and GLAHM V3363).

Other than the revision of Zittel's (1925) "Handbook of Palaeontology" already referred to, *Leedsichthys* received only one further mention from Smith Woodward. In February 1916, he described a new and particularly well-preserved specimen of the pachycormid *Saurostomus esocinus* from the Upper Lias of Baden-Württemberg (Smith Woodward 1916). He closed his description (Smith Woodward 1916: 51) with these words: "I may also add that some of the bones [of the *Saurostomus esocinus* specimen], such as the supraclavicle and the neural arches fused with their curved spines, are exact miniatures of some of the bones of the gigantic *Leedsia problematica* from the Oxford Clay. They therefore tend to support the opinion that this largest known Mesozoic Ganoid belongs to the Pachycormidae." Although Smith Woodward clearly felt that he had a far greater understanding of *Leedsichthys* than ever before, he did not (apart from the brief mention in the third edition revision of Zittel) mention the animal in print again.

Nor, indeed, was there any further mention of it in the literature until 1986. Then, as part of an overall work on the ecology of the Oxford Clay sea, Martill published a short piece comparing the bones of *Leedsichthys* to those of a particularly well-preserved and complete specimen of *Asthenocormus* (BMNH P.61563) recovered the preceding year from the brick pits near Peterborough (Martill 1986a). Martill used some of the bones (the individual caudal lobe length, the pectoral fin-rays, the hyomandibula and the gill arch apparatus) of the *Asthenocormus* specimen to attempt to calculate the full grown length of *Leedsichthys*. This technique echoed an earlier methodology employed on *Leedsichthys* – a label on display with the tail in 1937 noted that it measured some nine feet (approximately 2.7 metres) in depth (presumably including the painted fin-ray extensions that represented parts of the tail that were too thin to collect from the brick-pit). The label went on to say that "if the fish to which it belonged were of the same proportions as *Hypsocormus*...its total length must have been about thirty feet" (about 9.1 m). This text is likely to have been composed by Smith Woodward, and represents the earliest estimate of the animal's size. Interestingly, when this label was rewritten (it was on display in 1985 in its revised form, but it is unknown when the alterations were made), the estimated length was changed to "...about twenty-five feet" or 7.6 m. Martill's (1986a) application of this

methodology produced a range of possible full-grown sizes from 13.5 to 27.6 m. Martill presented a scaled reconstruction of the fish (drawn by Paul Pollicott) to this maximum estimate, which would, if supported, clearly make it the largest fish currently known to have ever existed. He also figured the tail specimen (BMNH P.10000) and a possible frontal (Peterborough Museum PETMG F.1). Martill (1988) went on to examine the ecology of *Leedsichthys* as a large filter-feeding 'baleen' whale analogue, and figured bones identified as a ceratohyal and a frontal.

Fragments of the branchial basket of *Leedsichthys* sp. from the Villers-sur-Mer region of Normandy, France, were described by Bardet *et al.* (1993), who interpreted the histology as indicating a high metabolism for this animal. A new occurrence of *Leedsichthys problematicus* was reported in an Oxford Clay fauna of northern Germany by Michelis *et al.* (1996), with a technique for distinguishing between the bones of *Leedsichthys* and marine reptile and dinosaur bones. Unfortunately, this technique appears to be somewhat erratic, as a bone of *Leedsichthys* was, in the same paper, again described as a caudal spine from a stegosaurid dinosaur (*Lexovisaurus* sp. – specimen WMfN PM 17006/8). This bone occurs in other specimens of *Leedsichthys* (e.g. GLAHM V 3363). A new species of *Leedsichthys*, *L. notocetes*, was described by Martill *et al.* (1999). This species was based on associated gill rakers contained within a limestone block (SMNK 2573 PAL) from the marine Callovian-Oxfordian Middle to Upper Jurassic strata of northern Chile (Martill *et al.* 1999). In the same year, Arratia & Schultze (1999) published on a completely different Oxfordian locality for *Leedsichthys* in Chile. Some 150-200 miles further south of the locality noted by Martill *et al.* (1999), at the opposite end of the Cordillera de Domeyko, these remains occurred in limestone concretions.

2.4 - ISSUES SURROUNDING THE TAIL SPECIMEN, AND ARCHIVAL CORRESPONDENCE

The tail specimen is particularly important to understanding what has been collected of this specimen. The structure of the large tail (BMNH P 10000) is the most compelling argument for the fish being pachycormid in nature, but in the absence of a published description of the tail (Martill 1986a), two damaging (if radically different) assumptions have historically been made. On the one hand, there is uncertainty over whether or not the tail can be attributed to *Leedsichthys problematicus*, as it appears to have been an isolated find, which has simply been referred to this species because of its great size. If this was the case, it would be improper, as it would ignore the possibility, however remote, that a second extremely large fish also existed as part of this fauna. At the other extreme,

assumptions have been made, since Smith Woodward's time, that the tail was part of the holotype material (Martill 1986a) – a label on display with the tail in 1985 stated unequivocally that "This tail is part of the HOLOTYPE described by A. S. Woodward in 1889." This is patently not the case, as testified to by the March 1898 letter. The text of the label is reworked from that which was on display in 1937, which significantly does not make the claim that the tail was part of the holotype material. It may well be that that particular myth proliferated solely from this revised label.

A review of archival correspondence (recently uncovered by Dr. Leslie Noè of the Sedgwick Museum, Cambridge University) between Alfred Leeds and staff of the NHM has recently brought to light a letter from Leeds that specifically refers to the discovery of the tail specimen. This letter, to A. S. Woodward, dated 18th March 1898 (correspondence in the Official Archives of The Natural History Museum, DF100/31), informs Smith Woodward of the discovery of a new specimen of *Leedsichthys* in one of the brick pits near Peterborough, and describes the general disposition of some of the bones around the site. These include a remarkably complete tail, which he hopes to excavate. This is undoubtedly BMNH P.10000, the only tail known, purchased by the NHM in March 1899, following extensive reconstruction by the Leeds family (Leeds 1956). What is critical, is that the letter (fig. 2.6) refers to other bones – pectoral fin-rays and "head bones" - being collected that are part of the same individual, and discusses them as bones of *Leedsichthys* that have been found before. This means that it is suddenly quite likely that the tail was found with bones comparable to the type material. Resolution of this question depends on identifying and examining the other material that arrived at the same time as the tail.

Fortunately, only four specimens of this animal, other than the tail, were purchased between the report in the letter of March 1898, and July 1905. All were purchased in July 1898, and only one (BMNH P.11823) features fin-rays and "head bones". It therefore seems likely that the bones of P.11823 (fig. 2.7), which arrived eight months before the tail, were registered separately, but nonetheless represent other parts of the skeleton belonging to P10000.

2.5 - ASSESSMENT OF MOST COMPLETE SPECIMENS FOR FUTURE STUDY

This does not, however, make P.11823/10000 the most complete specimen of this animal: the type material (BMNH P.6921) consists of considerably more remains. But the survey of known specimens also showed that one of the two specimens (fig. 2.8) bought by the

Hunterian Museum (GLAHM V3363) consisted of more than twice the quantity of material present in the type (Liston 1999). These three individuals – GLAHM V3363, BMNH P.6921, BMNH P.11823/10000 – appear to be the key individuals to reconstructing this animal and understanding its anatomy in future research.
The three individuals specified above all display a series of the bone morphologies highlighted by Smith Woodward in his initial 1889 description. How confident can we be that these three specimens are not conglomerations of individuals, rather than discrete entities? BMNH P.6921 is described in terms of being an "associated series of bones...spread over an area of probably not less than twelve square yards" (Smith Woodward 1889b: p.452) approximately 10 square metres, and it excludes one bone (BMNH P.6922) as "doubtfully forming part of the series" (Smith Woodward 1889b: 453). This would appear to indicate a rigour in Smith Woodward's allocation of registration numbers, careful not to associate material under one number unless he was absolutely certain that it all belonged to the same individual, despite the fact that these two sets of remains, it could be argued, very likely belonged to one individual alone.

The specimens purchased by the Hunterian Museum in January 1915 consist of two separate registration numbers, comprising a partial skeleton consisting of various elements (GLAHM V3363) and a single pectoral fin-ray (GLAHM V3362), an element that is not present within GLAHM V3363. If V3363 was an accumulation of separately found bones, then there would be little sense to not add the pectoral fin-ray to this assemblage, if one were simply selling a set of 'representative bones' to a museum. In addition, V3363 is replete with notes by A. Leeds relating to which of the packets related to the same bones, and which bones pair with each other. This would also seem to add weight to the given registration number representing a distinct individual.

The rationale behind regarding P11823/P10000 as one individual has been presented above, but the question of why different registration numbers would be accorded to the same individual still remains. The letter from Leeds to Smith Woodward refers to "the tail" lying a distance of "some 12 or 10 feet" (around 3-3.5 m) behind the pectoral fins. Perhaps, in the absence of an ossified axial skeleton connecting the two areas together, the NHM (possibly A. Smith Woodward himself) felt that it was safer to accession the other remains as distinct from the tail, to which they gave the special number of BMNH P.10000.

2.6 - IMPLICATIONS OF LETTER FOR FUTURE ESTIMATION OF SIZE

The letter of 18th March can be cautiously used as a basis for estimating the size of the *Leedsichthys* specimen found that day, in 1898, by A. Leeds. It gives distances, albeit rough, from the rear of the pectoral fins to the start of the tail, and dimensions for the tail as it lay in situ. The only other known indication for the disposition of different bone types of *Leedsichthys* prior to excavation, is the map of the site at Wallücke (Michelis *et al.* 1996), which only relates to the anterior portion of the body. Although described as having been subjected to some water-sorting, the larger elongate bones of the skull appear to have remained in situ, and one of the pectoral fins seems to have collapsed more or less in position. If this is the case, then it can perhaps be used to estimate the disposition of the elements of the anterior part of the body, and relate them to BMNH P.11823/10000, if common bones can be found between the two specimens.

In light of this, it appears worthwhile revisiting Martill's (1986a) methodology for assessing the overall size of the *Leedsichthys*. Martill's selection of *Asthenocormus* as a comparator taxon, a genus with a lower jaw lacking teeth, reflected the apparently toothless nature of *Leedsichthys*. His use of the complete specimen of *Asthenocormus* assumed that the ontogenetic development of the different parts of the three specimens of *Leedsichthys* used occurred in tandem with that of *Asthenocormus*, so that each bone maintained the same proportional significance with respect to the body length as it grew. This is unlikely. The use of the gill basket apparatus as a unit for scaling in particular must be questioned, as its size does not increase linearly with the size of a fish, as the physiological demands of the fish do not increase linearly with size. Although flawed (Martill 1988), the principle of the technique may well still be applicable, provided that common bones can be found between BMNH P.11823/10000 and the German specimen WMfN PM 17005, WMfN PM 17006, WMfN P 20238 etc.) represented in the site map (Michelis *et al.* 1996: fig. 5).

2.7 - CONCLUSIONS

The discovery of both the extraordinarily complete Glasgow specimen of *Leedsichthys*, and the letter from Alfred Leeds to Arthur Smith Woodward, helps to resolve the problems of understanding an animal that is only known from associations of bones that come from unmapped sites.

The lack of fully identified material has meant that for over a century, museums have only been able to describe their *Leedsichthys* material as gill-rakers, fin-rays, and miscellaneous skull bones (Leeds & Smith Woodward 1897) usually uncertainly identified as '?frontals'.

These developments finally offer some hope that the Glasgow specimen, in conjunction with the type material, can act as a 'Rosetta stone' to understanding the animal's anatomy, and enable many bone morphologies to finally be identified.

It may be seen that, if BMNH P.11823 is indeed the same individual as BMNH P.10000, then the problem over the disassociation of the tail from the rest of the individual was created by a number of circumstances. The absence of a formal scientific publication referring to it (which one might believe Smith Woodward fully intended to include as part of the Supplement to the 1895 Catalogue of the Fossil Fishes in the British Museum (Natural History)) was, of course, a missed opportunity. But also, the tail being sent eight months after the rest of the specimen, and being given a special registration number that kept it isolated from the rest of the material in the catalogue, would also have served to obscure the picture more.

2.8 - MATERIAL EXAMINED

The material mentioned in the text is held in the following institutions: BMNH, The Natural History Museum (London), England; SMC, Sedgwick Museum, Cambridge University, England; PETMG, Peterborough Museum & Art Gallery, England; GLAHM, The Hunterian Museum, University of Glasgow, Scotland; SMNK, Staatliches Museum für Naturkunde Karlsruhe, Germany.

The material referred to in the type description (Woodward 1889b) is BMNH P.6921 (associated series of bones), BMNH P.6922 (doubtfully part of the same associated series), BMNH 32581 (Vaches Noire specimen of associated gill rakers). Other material referred to in the text is BMNH P.10156 (the gill basket specimen), GLAHM V3363 (the Glasgow partial skeleton), BMNH P.10000 (the tail specimen from 1898), BMNH P.11823 (partial skeleton, also 1898).

Chapter 3

"Leedsia *is not quite such a problem to me as it was ten days ago - but still there is very much to learn"*

Alfred Leeds, 18th March 1898

Chapter 3

The tail of the Jurassic fish *Leedsichthys problematicus* (Osteichthyes: Actinopterygii) collected by Alfred Nicholson Leeds - an example of the importance of historical records in palaeontology.

3.1 - ABSTRACT

The specimen of the tail of *Leedsichthys problematicus* now in The Natural History Museum, London, was one of the most spectacular fossil vertebrates from the Oxford Clay Formation of Peterborough, but as an isolated find it shares no bones in common with the holotype of the genus and species. However, a letter from Alfred Nicholson Leeds and related documents cast valuable new light on the excavation of the tail, indicating that it was discovered with cranial bones, gill-rakers, and two pectoral fins, thereby including elements that can potentially be compared with those of the holotype. The documents also clearly indicate that The Natural History Museum specimen is not part of the same individual as any other numbered specimen of *Leedsichthys* as had been speculated on other occasions. The maximum size of the animal represented by The Natural History Museum specimen was possibly around 9.0 metres, considerably less than previous estimates of up to 27.6 metres for *Leedsichthys*. Historical documentary evidence should therefore be rigorously checked both when studying historical specimens in science, and in preparing text for museum display labels.

3.2 - INTRODUCTION

Documentary evidence is invaluable in the earth sciences, whether collectors' field sketches, specimen notes, correspondence, notebooks, draft manuscripts, photographs or specimen conservation records. However, when studying geological material, the specimens themselves, and previously published accounts of them, are of primary importance, and are often the only materials sought by researchers. Unpublished documents are only infrequently taken into consideration, but such original records can provide invaluable information on specimens and their provenance. Unfortunately, unpublished resources often reside separately from specimens, for instance in the stores of libraries or other dedicated archives, and the different wings of an institution may be entirely unaware of the existence and relevance of each other's resources. The relative obscurity of unpublished documents is reinforced by a tendency for historical studies relating to collectors (e.g. the Leeds brothers, in Leeds 1956) and researchers (e.g. Adam Sedgwick in Clark & McKenny Hughes 1890) to be published separately from the scientific study of their specimens.

As an example of the importance of searching for all possible sources of information when studying geological specimens, we present a letter and supplementary documents which shed considerable light on the most spectacular find of a fish from the Middle Jurassic Oxford Clay Formation in the vicinity of Peterborough, England – the gigantic tail of *Leedsichthys problematicus* Smith Woodward 1889[b] (P.10000; fig. 3.1)[1] .(Unless otherwise stated, all material cited is registered in The Natural History Museum, London [abbreviation = NHM], formerly the British Museum (Natural History) [abbreviation = BM(NH)].)

3.3 - *LEEDSICHTHYS PROBLEMATICUS* – AN ENORMOUS PROBLEM

Leedsichthys problematicus was a remarkable bony fish, a member of the Family Pachycormidae ('thick bodied'), which as a group lie close to the transition from the lower forms of ray-finned fish (Actinopterygii) to the teleosts that dominate today's seas. *Leedsichthys* has been described as "the world's largest fish" (Martill 1986a: 61), but despite (or perhaps because of) its immense size, it remains poorly understood (see Chapters 7 and 8). This is, in part at least, due to lack of study, the rarity of anything approaching a complete specimen, and incomplete skeletal ossification, resulting in poor preservation potential for significant parts of the body. The gigantic size of *Leedsichthys* and the lack of an ossified axial skeleton (Smith Woodward 1889b; Martill 1988) has probably led to finds in the field being regarded as isolated, when in reality some distance away articulated remains of the same individual lay undiscovered. This has probably been a major factor in why so many specimens of *Leedsichthys* only consist of isolated skeletal portions (see Martill 1988, and see also Liston 2004a for a supplementary list of finds). An additional problem is that uncertainty has attended virtually all osteological identifications of the skeletal elements of *Leedsichthys*, except for the bony fin-rays, and the gill-rakers (each approximately 7.5 cm long). Although gill-rakers appear to be the smallest of the bony remains of this fish, they are huge examples of fish gill-rakers, as these structures are usually only a few millimetres long. They line the gill arches of a fish, often facilitating the sorting of food from detritus as water passes through a fish's mouth and out of the gills (Sanderson *et al.* 2001). The size of these gill-rakers is such that they have been confused with the lower jaws of small tetrapods (e.g. pterosaurs, Martill pers. comm. 10/11/2003), but they occur with such frequency and are so distinctive in structure that they are considered the most diagnostic part of this fish (Smith Woodward 1889b; Martill, 1988; Martill *et al.* 1999). Our understanding of *Leedsichthys* is further clouded by the absence of any maps showing the in situ distribution of skeletal elements prior to removal for all but one of the collected specimens (see Michelis *et al.* 1996), and the tendency for previous

workers to ascribe all large, fibrous-textured skeletal elements from the Oxford Clay Formation to *Leedsichthys*, although many pliosaurian and dinosaurian bones also apparently demonstrate such textural features (Martill 1988; Noè *et al.* 2003). Furthermore, workers have ascribed *Leedsichthys* bones to other, non-fish, taxa such as dinosaurs and marine reptiles (e.g. Hulke 1887; von Huene 1901; as noted in Hoffstetter 1957) and this has further complicated resolution of the anatomy of this enigmatic fish.

3.4 - THE DISCOVERY OF LEEDSICHTHYS: THE HOLOTYPE AND BEYOND

A substantial proportion of an enormous fish was discovered in the 1880s in one of the many brickpits near Peterborough (Leeds & Smith Woodward 1897; Leeds 1956). The exact location of this pit is not recorded, but the find was presumably in the Peterborough Member of the Oxford Clay Formation (Cox *et al.* 1992; Martill 1986a, 1988; Liston 2004a), and therefore Callovian (Middle Jurassic) in age. The bones were ascribed to a single disarticulated individual and were found scattered "over an area of probably not less than twelve square yards" (ca. 10m²) of a single bedding plane (Smith Woodward 1889b: 452). They were excavated by Alfred Nicholson Leeds (1847-1917; Smith Woodward 1917) and were added to his extensive private collection (Leeds 1956). Misidentified as stegosaurian armour, the material was recognised as "piscine" rather than dinosaur by Othniel Charles Marsh (1831-1899; Woodward 1899), when he visited Alfred Leeds in 1888 (Smith Woodward 1889b) as part of a tour around Europe to review all key dinosaur material (Marsh 1889). Smith Woodward now described and named the specimen as *Leedsichthys problematicus*, tentatively identifying the principal bones of the specimen (P.6921) as a frontal, an angular, a hyomandibular, four branchial arches, a large number of gill-rakers, an incomplete preoperculum or clavicle, eleven branchiostegal rays, and a series of pectoral fin-rays (Smith Woodward 1889b: 451-454; 1889c; 1890a), although several other interpretations have subsequently been made (Smith Woodward 1895; Liston 2004a). The jaws and axial skeleton were apparently absent. The original description failed to figure any of the material, but did note a few further isolated specimens not associated with the holotype (including one described as "doubtfully forming part of the series" Smith Woodward 1889b p.453), but considered too fragmentary to be satisfactorily identified (Smith Woodward 1889b). Two of the distinctive gill-rakers from the holotype were subsequently figured, and the name *Leedsichthys problematicus* "conveniently shortened" to Leedsia problematica (Smith Woodward 1890b: 292). However, such a name change is not valid, and creates an unwarranted junior objective synonym (ICZN 1999), so the original name *Leedsichthys problematicus* Smith Woodward 1889[b] must remain (Martill 1986a, 1988; Liston 2004a). Soon afterwards, all of Alfred Leeds' 'First

Collection' (collected up to about May 1889), including the holotype of *Leedsichthys problematicus*, was purchased by the British Museum (Natural History) (now the Natural History Museum, London) in four instalments between 1890 and 1892 (Leeds 1956). Following its arrival at the BM(NH), the holotype of *Leedsichthys* was assigned the registered number P.6921, and the "doubtfully" associated specimen was given the registered number P.6922.

As well as the holotype of *Leedsichthys*, Alfred Leeds also collected the largest caudal fin of a fossil fish on record (P.10000, fig. 3.1), comprising both caudal lobes, although their orientation (i.e. which is superior and which is inferior; Martill 1988) and the angle at which they met is not known. P.10000 has been referred to *Leedsichthys problematicus*, or its junior synonym *Leedsia problematica* (Smith Woodward 1905, 1917; Leeds 1956; Martill 1986a). As preserved, it spans "9 feet" [ca. 2.7 m] (Smith Woodward 1917, p.480). However, when discovered, the tail measured around "6 feet" [ca. 1.8 m] along one of the lobes, although the full extent could not be collected because distally the fin-rays became too thin and fragile to gather (Leeds 1956, p.73).

3.5 - A TAIL OF MANY PROBLEMS

P.10000, the tail referred to *Leedsichthys*, presents a number of problems: the size of the original fish; the taxon to which the specimen belongs; the date of collection of the specimen; and historical confusion about possible relationships between it, the holotype and other *Leedsichthys* material.

The holotype of *Leedsichthys problematicus* is undoubtedly P.6921 (Leeds 1956; contra Martill 1988 who erroneously referred to and described P.10156 as the holotype, for reasons explained later). Confusion has been compounded by a suggestion that P.10000 is part of the same fish as the holotype (Martill 1988), although this is most likely to be in reference to P.10156, as the true holotype (P.6921) was omitted from the list of material attributed to *Leedsichthys*. Martill *et al.* (1999) also tentatively suggested that the tail is from the same fish as P.10156 (erroneously referred to therein as P.10561), comprising a gill-basket and hyomandibula. More recently Liston (2004a) proposed that P.10000 is associated with P.11823, which consists of head bones and fin-rays. Whether these specimens of *Leedsichthys* are parts of one or more individuals is of paramount importance for our understanding of the fossil material, and as P.10000, P.10156 and P.11823 each have different accession numbers (Martill 1988) this implies they were acquired by the

BM(NH) at different times, and were therefore considered discrete individuals when purchased and accessioned.

The date of collection of P.10000 has been cited as both 1889 (Martill 1986a: 61) and 1899 (Leeds 1956: 72; Martill *et al.* 1999: 249) and this imprecision causes confusion in relation to the tail specimen. It is known that P.10000 was mounted and on display in the BM(NH) fish gallery by 1905 (Smith Woodward 1905), but details of the specimen and its excavation were not published until long after the death of Alfred Leeds in 1917 (Leeds 1956). Despite its obvious importance, P.10000 was not figured for more than eighty years after its collection and public display (Martill 1986a), and has never been fully described, although ongoing work (by JJL) aims to rectify this.

Although referred to *Leedsichthys* (Smith Woodward 1905; Leeds 1956; Martill 1986a, 1988), the tail (P.10000) as an isolated find (Leeds 1956), shares no elements in common with the head and pectoral components of the holotype (P.6921; Martill *et al.* 1999). Indeed, the tail appears to have been assigned to *Leedsichthys* based solely on its large size, fibrous bone texture, and fin-rays that branch without segmentation (the latter a diagnostic character of pachycormid fish (Martill 1988)). However, these criteria are clearly unsatisfactory, and a more precise diagnosis is desirable.

3.6 - UNPUBLISHED DOCUMENTARY EVIDENCE

In addition to some privately held items, a series of searches of the Natural History Museum Official Archives[2] has recently uncovered unpublished documents relevant to these problems. These include: a letter from Alfred Leeds, Natural History Museum purchase and accession registers, and historical photographs showing the labelling of the specimens.

3.6.1 - Alfred Leeds' letter

A handwritten letter[3] from Alfred Nicholson Leeds to Arthur Smith Woodward (1864-1944; Cooper 1945), dated 18 March 1898 (fig. 3.2, text reproduced by permission of the Trustees of The Natural History Museum), announced the discovery of a new specimen of 'Leedsia' (the junior synonym of *Leedsichthys*). The letter (NHM Official Archives DF100/29-30) is transcribed below (text reproduced by kind permission of the Trustees of The Natural History Museum):

> Eyebury 18th March 1898.
>
> Dear [Arthur Smith] Woodward -

> Leedsia is not quite such a problem to me as it was ten days ago - but still there is very much to learn - the men came across some more of its bones at one of the pits - and sent for me to get them out - I feel certain now that all the bones we thought belonged to the head, are head bones - for they were all mixed up with thousands of gill-rakers - then just beyond the head I found a good distance apart two fins - I got part of one out + can put some of it together - but only some for it was in thousands of pieces - then away back some 12 or 18 feet they came upon the tail - [fig. 3.3] as it lay in the clay from A to B, was about 6 ft - + from B to C the same - those long branching bones which you have from 3 ft to 4 ft long form the tail – which from D to E is about 18 inches wide - + about 1¾ thick - I have got a great lot of the tail that I can put together - for though of course it is all separate bones - some three or four feet of it is all in a mass held together by the clay which has turned to stone between the bones and I hope to have a piece of tail, some five feet long + one + a half wide - when I have done - it was quite impossible to do any thing with about a foot quite at the end for the pieces were too small to pick up - much more to fit - At present I have got none of the big rib shaped + long straight bones - but live hoping they may come across them - but it is quite clear they have nothing to do with the head - I incline to the idea that they form the back fin - + that the straight bones may be inside + help to support them – thus [fig. 3.6] I have not seen the least sign of any thing that could be called vertebrae - I've a great number of bones to wash yet - + it will take months to fit them - but I'll let you know as soon as they are in condition for your inspection - tell Dr. [Henry] Woodward he will have to keep something in hand for this lot - but I think he will want a larger case to hold them - I do hope I'll get the big rib shaped bones - I've told the men to send for me if they come across them so that I may see how they lie -
>
> Yours very sincerely
>
> Alfred. N. Leeds.

In addition to the approximate distances given between some elements as they lay in the clay, Leeds also gave a roughly dimensioned sketch of the tail (fig. 3.3). Unfortunately, in spite of the hopes of Alfred Leeds, there is no evidence to indicate additional finds of skeletal elements were forthcoming from this site. Although this letter was annotated as being acknowledged on the "21st" [March 1898], no reply from Arthur Smith Woodward

survives, as the BM(NH) Palaeontology Department outgoing letter archives only began in 1902.

3.6.2 - Purchase and accession registers

Purchase and accession registers contain information relevant to some of the issues surrounding P.10000. The purchase register records the acquisition of five batches of *Leedsichthys* bones from the Leeds family, on 30 May 1892[4] (the final instalment of his 'First Collection'), 28 July 1898[5], 17 March 1899[6], 22 July 1905[7] and 28 June 1920[8], as well as indeterminate fossil fish plates[9] (see Table). The bones of the tail, purchased on the 17 March 1899, are described as "a set of fish remains of Leedsia problematica [sic] Oxford Clay Peterborough". The sale was sanctioned by the Trustees on 25 February 1899 for the purchase price of £ 25.0.0[6]. The accession register records the specimen numbers allocated to material, and also gives indications as to which year this allocation was made in. For example, specimen P.10000 is recorded as "Leedsia problematica [sic] Oxford Clay, Fletton, Peterborough, tail and associated bones Purch[ase]d A.N. Leeds, Esq. March 1899"[10]. The P.10000 entry in the accession register is out of chronological order with the adjacent lower and higher numbered entries, giving weight to the suggestion that the 'special' number P.10000 had been reserved for this spectacular tail (Martill 1986a – although Martill (pers. comm.) can no longer trace his source for this comment). There are separate entries in the accession register for all other *Leedsichthys* specimens purchased from Alfred Leeds, the purchase dates recorded there closely coinciding with those in the relevant purchase registers (see Table 3.1). However, these and other non-*Leedsichthys* specimens are also not necessarily numbered in the order they were acquired by the Museum, demonstrating that the 'out of sequence' occurrence of P.10000 was not in itself a unique event.

3.6.3 - Photographs

Two photographs exist of P.10000, as it was mounted for display in the fossil fish gallery of the then British Museum (Natural History), revealing details of the labelling on display with the tail. The first was taken in September 1937[11] (fig. 3.4); the label indicates an estimated length of "30 feet" [ca. 9.1 m], the same as the earliest known published size estimate (Smith Woodward 1905, 1917; see also Leeds 1956). A second photograph (fig. 3.5), taken during a visit by David Martill in July 1985, shows that the label had by that time been altered, reducing the proposed length of the animal to "25 feet" [ca. 7.6 m], whilst adding "the tail is part of the holotype described by A. Smith Woodward in 1889".

3.6.4 - Additional Documentation

The Minutes of the Trustees' Meeting of 25/2/1899, under 'Purchases Geology', note the sanctioning of a purchase of "a set of huge fish remains" from the Oxford Clay from Mr. A. N. Leeds, for £25.00[12]. Three further documents relate to this meeting and P.10000. A short list, dated 21/2/1899, written and signed by Alfred Leeds[13] offers "a series of large bones of Leedsia problematica [sic] [including a] fragment of pectoral fin [for] £ 25.0.0". This document also includes a rough sketch of what appears to be the pectoral fin in question. A second, undated, note[14] in the hand of Henry Woodward (1832-1921, British Museum (Natural History) Keeper of Geology; Anonymous 1921), probably a very early draft of the next item, indicates the *Leedsichthys* tail specimen consists of a "Fine associated set of remains...comprising several of the head bones of gigantic size, a fragment of the pectoral fin, and the greater part of the tail fin. The latter so far as preserved, measures about 9 ft. [ca. 2.7m] in span, and would probably have measured originally at least 12 ft. [ca. 3.7m]. It seems to be the largest caudal fin of a fish on record." A third, also undated, but much longer manuscript in the hand of Henry Woodward[15] recommends a series of purchases to the Trustees. In relation to the tail specimen, Henry Woodward states "Mr Leeds offers [the Trustees] a fine associated set of remains of Leedsia problematica [sic] a gigantic fish from the Oxford Clay of Peterborough", that the bones are "of enormous size", and gives the dimensions of the tail as "about 9 feet and was probably originally 12 feet in span" [ca. 2.7 m and 3.7 m respectively]. Henry Woodward again notes of the tail that "it seems to be the largest caudal fin of a fish on record". These three documents are indisputably linked in all referring to unique dinosaur material offered and approved for purchase along with the tail and associated bones at the same Trustees' Meeting. As the British Museum would not have been agreeing to purchase a specimen eight months after it had been delivered (there are no examples of Alfred Leeds ever sending material on approval – on the contrary, it appears the British Museum staff frequently visited Eyebury house to assess new discoveries with a view to possible purchase), it seems most likely that the July 1898 acquisition of material is entirely unrelated to the specimen found by Alfred Leeds in March 1898, and offered for sale the following February.

Three letters to or from Edward Thurlow Leeds (1877-1955; MacGregor 2001), the son of Alfred Leeds and later curator of the Ashmolean Museum in Oxford, also relate to P.10000. Considerable time was spent by E.T. Leeds amassing information on his father and the Leeds Collection, with a view to publishing a book on the subject (Leeds 1956). Whilst compiling the material, E.T. Leeds wrote numerous letters to the BM(NH)

enquiring about the acquisition of the Leeds Collection, dates of visits of Alfred and his brother Charles to the Museum, and requesting photographs of specimens for inclusion as plates in the final version of the manuscript. A letter from E.T. Leeds[16] requests a photograph of P.10000, but the reply from WDL[17] (Dr William Dickson Lang; 1878-1966; White 1966) indicated that no photograph of the tail specimen had ever been taken, and that it would take some time (probably a few months) for one to be made. The third item, a card from E.T. Leeds[18], indicated that a copy of "the excellent photograph" had arrived, undoubtedly referring to the 1937 photograph[11] of P.10000 (fig. 3.4), which is the only photograph of the tail in the NHM's archives. Some of the mass of data collected by E.T. Leeds about his father and the Leeds Collection was posthumously edited and published (Leeds 1956), and the original manuscript has recently been traced by the authors, still held by a member of the Leeds family. This discovery will permit further important archival work to be undertaken on the Leeds Collection fossils, but more immediately it has allowed confirmation that the photograph of the tail that E. T. Leeds used for a plate in his original manuscript matches the image held in the NHM archives, thus dating the photograph precisely to September 1937.

3.7 - DISCUSSION

Alfred Leeds' 1898 letter[3] and the associated documents held by the NHM[4-18] resolve some, but not all, of the problems relating to the tail attributed to *Leedsichthys problematicus* (P.10000). That Alfred Leeds' letter refers to P.10000 is beyond doubt. All the documents indicate the tail specimen (P.10000) was part of the Leeds Collection, and no other tail consisting of more than a single fin-ray attributed to *Leedsichthys* is known, or was collected by Alfred Leeds: E.T. Leeds refers to it as "**the** tail" (Leeds 1956, p.75 our emphasis), and records the undertaking by the Leeds family never to collect or reconstruct a tail of this fish again. The letter resolves the confusion over the date that P.10000 was collected. Both previously cited dates are erroneous (1889 by Martill 1988; 1899 by Leeds 1956 and Martill *et al.* 1999) as P.10000 was excavated during March 1898. The idea of 1899 as the year of collection (Leeds 1956; Martill *et al.* 1999) probably arose from the label visible in the 1937 photograph taken by the BM(NH) and sent to E.T. Leeds[11] (fig. 3.4), which in turn probably refers to the date of arrival noted in the NHM purchase register[6] (indeed, the handwritten manuscript for the Leeds Collection book by ET Leeds (1939), entitled 'Eyebury and the Leeds Collection' and dating from 1938/9 records an initial date of 1904, scored out and later altered to 1899 – 1904 might well reflect a memory of ETL relating to the collection of the gill basket specimen BMNH P.10156). Assuming that it is not the result of a typographical or proof-reading error, the 1889 date

(Martill 1986a) is likely to have arisen from the misleading information on the label on display with the tail in the BM(NH) in 1985 (fig. 3.5) indicating that P.10000 formed part of the holotype. The delay between the date of collection (March 1898) and the date of purchase by the BM(NH) (March 1899) is hinted at in Alfred Leeds' letter: "I've a great number of bones to wash yet - + it will take months to fit them"[3], and this is corroborated by the work required to "fit literally thousands of fragments" by Alfred Leeds and his family (Leeds 1956: 74).

3.7.1 - Associated bones

Alfred Leeds' 1898 letter[3] demonstrates that when collected the tail was associated with other bones, and was therefore not found in isolation (contra the description in Leeds 1956, written by one of Leeds' sons, who apparently was not present at the excavation). The purchase and accession registers[6, 10], together with unnumbered documents in the NHM[13-15], confirm that the associated bones were all acquired by the BM(NH) in March 1899, although the tail, and currently only the tail, has the registered number P.10000. The associated skeletal elements (cranial bones and a partial pectoral fin) have yet to be located, but the specimens clearly reside within the NHM, either unlabelled or under a separate registered number. This assumes that the missing parts have not decayed, been de-accessioned, or otherwise disposed of, although there is no evidence (such as annotations in the accession register) for any of these latter suggestions.

Alfred Leeds' letter[3] and associated documents[4-18] also resolve the problems of the proposed associations between P.10000 and other NHM *Leedsichthys* material. The tail cannot be associated with the holotype of *Leedsichthys problematicus* (P.6921), which was part of Alfred Leeds' 'First Collection' acquired by the BM(NH) between 1890 and 1892 (Leeds 1956), and well before the discovery of P.10000 in March 1898. The probable source of this proposed association (Martill 1988) is indicated by the differences of labelling on display in 1937 and 1985 in the BM(NH). Unlike the 1937 photograph of the tail[11] (fig. 3.4), the label visible in the 1985 photograph (fig. 3.5) incorrectly describes P.10000 as part of the holotype of *Leedsichthys*. There is no record of when this change of labelling took place (although a check of the relevant departmental minutes may well prove fruitful in this regard), but Alfred Leeds' 1898 letter, and the purchase and accession registers for both the holotype (acquired 1892[4]) and the tail specimen (acquired 1899[6]), clearly demonstrate this modification was incorrect. Examination of the NHM purchase and accession registers also precludes the tail (P.10000) from being associated with the gill-basket (P.10156; also incorrectly labelled as the holotype in the BM(NH) in 1985), as

understood by Martill (1988). The tail specimen (with its non-tail components) was purchased and transported in its entirety in March 1899, and P.10156 was a separate purchase in July 1905, thus, P.10000 (the tail specimen) and P.10156 have distinct years of purchase and different accession numbers. Thus, speculation that these two specimens are part of the same individual (Martill 1988; Martill *et al.* 1999) can be rejected. The confusion probably arose from the incorrect labelling of both P.10000 and P.10156 as the holotype whilst on display. This forms an unusual contrast to the more commonly encountered scenario (e.g. as presented in Torrens 1979), whereby a type specimen lies unrecognised and presumed lost in a collection. Here we have the far more rare and unlikely situation of a 'cuckoo specimen' usurping the role of the original holotype material of a species, on the basis of no apparent evidence whatsoever, when the real holotype was still safe and known to be in the same institution's collections. The usurper was then unambiguously and publicly advertised as part of the holotype, thus becoming imbued with a taxonomic importance that it simply should not have been accorded (particularly as it appeared to lack any of the components designated in the published type description).

The proposed association between P.10000 and P.11823 is more difficult to resolve. The tail, P.10000, was discovered in March 1898, and P.11823, which apparently contains many of the same elements as the missing parts of P.10000 (Liston 2004a), was purchased on 28 July 1898[5]. P.11823-11826 are described in the purchase register simply as "various bones of Leedsia [sic] &c", but the specimens were not allocated accession numbers (or given individual osteological identifications) in the accession register until after specimens purchased in 1915[5]. However, the note from Alfred Leeds' offering the tail specimen for sale[13], the two documents written by Henry Woodward[14, 15], and the purchase and accession registers[6, 10] all indicate the tail was purchased with its associated bones; some of the documents corroborate Alfred Leeds' letter[3] by specifying head bones and an incomplete pectoral fin, as well as showing that the specimen was purchased at the same time as unique dinosaur material. Thus, despite the lack of detail in the NHM purchase and accession registers, and no additional documents relating to the purchase of P.11823, an association with P.10000 can be rejected. P.10000 and P.11823 must therefore be considered as separate individuals of *Leedsichthys* (contra Liston 2004a).

Alfred Leeds' recognition of the presence of cranial bones and gill-rakers associated with P.10000, regardless of their current accession numbers, is of considerable importance as these osteological elements coincide with elements of the holotype of *Leedsichthys*

problematicus (P.6921). The gill-rakers in particular are of paramount importance, especially as *Leedsichthys notocetes* Martill *et al.* 1999 was designated solely on the basis of differences in the morphology of gill-rakers preserved in a cluster from east of Antofagasta, in the Atacama Desert of Chile. In addition, Alfred Leeds had carefully collected, washed, and reassembled the bones of the holotype (P.6921), the tail and associated bones (P.10000), and several other specimens of *Leedsichthys problematicus* (see Table 3.1), learning "to recognise the individual features of every bone with which he had to deal" (Leeds 1956: 23). Thus, Alfred Leeds was more familiar than anyone else with the bones of *Leedsichthys*, and even in the present-day absence of the P.10000 associated material (which remains to be identified in the NHM), Alfred Leeds' 1898 letter[3] adds considerable weight to the assignation of P.10000 to *Leedsichthys problematicus*, an assignation we provisionally accept here. However, this proposed assignation can only be confirmed or refuted once the bones associated with the tail have been located, identified, and compared with those of the holotype (P.6921).

In his 1898 letter[3], Alfred Leeds notes "I feel certain now that all the bones we [presumably Alfred Leeds and Arthur Smith Woodward] thought belonged to the head, are head bones – for they were all mixed up with thousands of gill-rakers". Although the anatomical identities of the individual head bones remain unresolved (Smith Woodward 1889b, 1895; Martill 1988; Liston 2004a), Alfred Leeds' letter reinforces the opinion that the large flat bones assigned to the cranium (Smith Woodward 1889a) were indeed derived from the head. Alfred Leeds in his 1898 letter also notes the absence of "big rib shaped + long straight bones" previously discovered with *Leedsichthys*. Alfred Leeds suggests that these bones have nothing to do with the head, but may form part of the (presumably absent) dorsal fin (fig. 3.6). It is hoped ongoing work (by JJL) will confirm or refute this suggestion. Alfred Leeds also notes the absence of vertebrae in this specimen, corroborating the suggestion that *Leedsichthys* had limited ossification of its axial skeleton (Smith Woodward 1889b; Leeds 1956; Martill 1988), a trend also seen in other pachycormid fish.

3.7.2 - Estimated size

The size of *Leedsichthys problematicus* is unknown (Martill 1988), but published estimates all agree it was "a very large fish" (Smith Woodward 1889a: 31). The length of *Leedsichthys* was estimated by Smith Woodward as probably being about "30 feet" [ca. 9.1 m] (Smith Woodward 1905, 1917; Leeds 1956). Subsequent length estimates have ranged from 10.5 to 27.6 m (Martill 1986a), suggesting *Leedsichthys* was "perhaps the largest fish

of all time" (Martill & Hudson 1991: p.30). However, the 1986 calculations were derived by scaling up a complete, approximately 1.75 m long, specimen of the pachycormid putatively identified as *Asthenocormus* (P.61563), to match isolated elements from different specimens of *Leedsichthys* (Martill 1986a, 1988). Currently, this scaling exercise is the only published size estimation technique for *Leedsichthys*, and all subsequent estimates have been based on these calculations (Martill 1988; Martill 1991; Martill & Hudson 1991; Bardet *et al.* 1993; Martill, Taylor & Duff 1994; Martill *et al.* 1999). However, as no substantially complete specimen of *Leedsichthys* has yet been described, and as different parts of the same individual gave sizes ranging from 13.5 m to 27.6 m (Martill 1988), such estimates must remain conjectural. Despite these problems, it is clearly desirable to have accurate size estimations in order to appreciate the anatomy, biomechanics, ecology and trophic position of this colossal fish.

Alfred Leeds' letter[3] also provides approximate dimensions for the P.10000 tail specimen of *Leedsichthys* as it lay in the ground. The letter thereby provides only the second in situ bone disposition information for a specimen of *Leedsichthys* (see also Michelis *et al.* 1996), and is a unique record of remains that were evidently substantially complete.
In his March 1898 letter, Alfred Leeds states that "just beyond the head" and "a good distance apart" were two fins, and that "back some 12 or 18 feet [approximately 3.6 m and 5.5 m respectively] was found the tail"; a sketch of the tail is provided with dimensions (fig. 3.3). There are, however, a number of problems with interpretation of the measurements given by Alfred Leeds, the most important of which are: no sense is given of the size of the head or the distribution of the bones; the dimensions given are very approximate; and the disposition of the postcranial elements as described could be interpreted in a number of ways. However, by assuming the fish lay articulated in the clay (as Alfred Leeds appears to interpret the remains), and that the two fins referred to were the paired pectorals lying as though still connected to either side of the body, an estimate of how the remains were discovered can be inferred (fig. 3.7). From this plan, the maximum dimensions for this fish can be estimated by taking Alfred Leeds' 18 feet [ca. 5.5 m] maximum body length and adding: 0.5 metres anteriorly for the "short distance" from the head to the fins; a further 0.5 metres for the proximal length of the pectoral fins; and at least 1.5 metres for the anteroposterior length of the tail. This gives an estimated body length of 8.0 metres plus a head of unknown dimensions, but a conservative estimate of 1 m for the head would give a maximum estimated overall length of 9.0 metres. This figure is remarkably close to the length estimated for *Leedsichthys* based on P.10000 of about 30 feet [ca. 9.1 m] (Smith Woodward 1905, 1917; Leeds 1956); which (if the above

interpretation of the letter is correct) might suggest the possibility that Smith Woodward's (1905, 1917) size estimation was based on Alfred Leeds' letter and/or personal communication between the two men. A more recent estimate of 14 metres for *Leedsichthys* has been proposed by comparison between the lengths of the caudal fins of '*Asthenocormus*' (P.61563) and the 1.8 metre length of the P.10000 tail lobes (Martill 1986a). Although flaws in the technique were recognised (Martill 1988), scaling from a fish with tail lobes of 250 mm to a fish with tail lobes of over 1.8 metres is fraught with difficulties and potential errors. Thus 14 metres may well be an overestimate for this individual of *Leedsichthys*.

3.8 - CONCLUSIONS AND WIDER IMPLICATIONS

Alfred Leeds' letter of 18 March 1898[3], together with the supplementary documents (purchase and accession registers[6, 10], archive photographs[11], notes and other documents[13-18]) held by the NHM GL and NHM ESL, had not previously been recognised as referring to P.10000, the only tail of *Leedsichthys* known. These documents are of considerable importance as they cast valuable new light on the discovery and interpretation of P.10000, and thus add significantly to our understanding of *Leedsichthys problematicus*:

The date of collection of P.10000 and its associated material was March 1898, refuting both previously published collection dates (1889: Martill 1986a; and 1899: Leeds 1956; Martill *et al.* 1999);

The tail is confirmed as measuring about six feet [ca. 1.8 m] along each lobe when discovered (Leeds 1956);

The tail, now registered under the number of P.10000, was found associated with cranial and pectoral elements, most of which were recovered and probably still reside in the NHM;

Alfred Leeds, who was intimately familiar with *Leedsichthys*, assigned P.10000 to *Leedsichthys problematicus* based on more than just the tail. However, confirmation of the taxonomic identity of P.10000 will have to await rediscovery of the associated material in the NHM, and comparison with the holotype of *Leedsichthys* (P.6921);

P.10000 is not part of the same individual as the holotype (P.6921), or any other numbered individual of *Leedsichthys problematicus* (P.10156, P.11823);

The bones of *Leedsichthys* believed to belong to the head (Smith Woodward 1889b) probably do so; other long rib-like bones (lacking in P.10000) may be the dorsal fin supports; the vertebrae were probably cartilaginous with poor preservation potential and hence absent from this specimen;

The maximum size of P.10000 may have been around 9 metres. Discussion between Alfred Leeds and Arthur Smith Woodward regarding the size of this specimen may well have informed the earliest published size estimate for *Leedsichthys*;

The size determination obtained for P.10000, by comparison with the tail of '*Asthenocormus*' (Martill 1986a), may thus be an overestimate, confirming that the scaling technique used was unreliable.

The importance of Alfred Leeds' letter[3] and the associated documents relating to P.10000 cannot be overstated. Had it not been for the existence of Alfred Leeds' letter to Arthur Smith Woodward, the association of the skeletal elements found with the tail would have been lost forever, and incorrect associations would have continued to be assumed, potentially leading to further unsound conclusions.

The lessons from this palaeontological example of the importance of archival resources can be applied more widely to the Earth Sciences, and beyond. In order to gain all possible information from historical specimens, all sources of documentation, both published and unpublished, should be sought and consulted in order to gain the fullest possible understanding of the material under study.

3.9 - Chapter 3, Endnotes

[1] The fossils and documents referred to are located in The Natural History Museum, Cromwell Street, London SW7 5BD (NHM).

[2] The Official Archives of the NHM, held by the General Library (GL) and Earth Sciences Library (ESL).

[3] Letter from Alfred Nicholson Leeds to Arthur Smith Woodward 18 March 1898; Correspondence section NHM GL DF100/31.

[4] Geological Department annual purchases register volume 2, 1892-1948; NHM GL DF102/2: 4.

[5] NHM GL DF102/2: 73.

[6] NHM GL DF102/2: 79.

[7] NHM GL DF102/2: 134.

[8] NHM GL DF102/2: 229.

[9] NHM GL DF102/2: 10.

[10] Palaeontology Department specimen catalogues, additions to the collection of fossils, Pisces Vol. 3A; NHM unnumbered.

[11] NHM ESL negative number 1660.

[12] NHM ESL DF103/40: 25.

[13] A. N. Leeds "Mr Leeds' Dinosaur", dated 21 February 1899 (1 folio); ms NHM-ESL unnumbered.

[14] H. Woodward "Fine associated set of remains . . .", not dated (1 folio); ms NHM-ESL unnumbered.

[15] H. Woodward "The Keeper of Geology has the honour to report . . .", 3pp., not dated (3ff); ms NHM-ESL unnumbered.

[16] E. T. Leeds to W. D. Lang, 21 August 1937, NHM GL DF100/154/7.

[17] W. D. Lang to E. T. Leeds, 25 August 1937, NHM GL DF100/154/7.

[18] E. T. Leeds to W. D. Lang, 19 September 1937, NHM GL DF100/154/7.

3.10 – ADDENDUM

Subsequent to the publication of this chapter in the Archives of Natural History, material almost certain to be the missing parts of BMNH P.10000 have been tracked down amongst the fossil fish collections (see Appendix IX for further details).

Chapter 4

"But that was in another country, and besides, the [fish] is dead."

The Tragedy of the Rich Jew of Malta (act IV scene i)
Christopher Marlowe 1589

Chapter 4:

The Occurrence Of The Middle Jurassic Pachycormid Fish *Leedsichthys*.

4.1 - ABSTRACT

A review of the occurrences of the Middle Jurassic pachycormid fish *Leedsichthys* is presented, including a new French locality. The variety of past misidentifications of these remains is noted, and the bones reinterpreted according to information derived from the broader hypodigm of material available for study. Trace fossils from the Lower Callovian outside Basel in Switzerland are assessed with regard to *Leedsichthys*, in addition to a review of relevant body fossil material from France, Germany and Chile.

4.2 - INTRODUCTION

Although first described in 1889, a number of historical misidentifications of its bones have hindered the spread of awareness of the osteology of *Leedsichthys*, leaving this animal obscure. Of the few published works that have dealt with *Leedsichthys*, most have concentrated on material collected from the Callovian Oxford Clay around Peterborough. In this paper, some of the more commonly misidentified elements will be noted with reference to their likely position in the skeleton of *Leedsichthys*, with particular emphasis being given to material coming from localities outwith the vicinity of Peterborough in England. A summary of specimens referred to in detail is presented in Table 4.1. This work is a prelude to a broader reassessment of all identified skeletal elements of *Leedsichthys* (see Chapter 8).

4.3 - EARLY ENGLISH DISCOVERIES

Up to the time of the first discovery of *Leedsichthys*, the Callovian Oxford Clay around Peterborough (fig. 4.1) had yielded large reptile bones for many years (Porter 1861), mostly through the endeavours of the fossil-collecting gentleman farmer Alfred Nicholson Leeds (Leeds 1956). The fact that reptilian remains were known to be reasonably common, combined with the unusually large, thin and flat quality of a new set of bones, led to the first describer appending *Leedsichthys* bones to a description of some stegosaur bones from the same clay (Hulke 1887). Hulke also incorrectly described the material as coming from the Kimmeridge Clay (Kimmeridgian in age, 154.7-152.1 mya), when it was actually from the older Callovian Oxford Clay (157.1-167.3 mya) around Peterborough (Harland *et al.* 1990).

In attributing these fossilised remains to a stegosaur, the reasoning of Hulke was that these large plate-like bones resembled the armour plates described from the back of *Stegosaurus* from the Jurassic deposits of the Rocky Mountains of the United States by Othniel Charles Marsh (Marsh 1880, 1881, 1887). The year after publishing his analysis of the dermal armour of *Stegosaurus* (Marsh 1887), Marsh himself visited England. He had spent the previous ten years collecting large quantities of dinosaur material in the United States, and was now touring Europe to review all the dinosaur material he could track down, for comparative purposes (Marsh 1889). Hulke's paper had attracted Marsh's attention, and he wished to examine the dinosaurian remains in Alfred Leeds' collection, including those identified as dermal plates of a stegosaur. The question, raised by Hulke (1887) was whether or not the Peterborough *Omosaurus* was congeneric with the North American *Stegosaurus*. Marsh travelled to the Eyebury home of the collector Alfred Leeds to see the material ('OC Marsh from Yale' is noted in the Eyebury visitors' book as visiting on 22nd August 1888, in the company of Henry Woodward, Keeper of the Department of Geology, British Museum (Natural History) (Anonymous 1921)), and declared emphatically that the plate-like bones in question were in fact "piscine" in character (Smith Woodward 1889b: p.452). Such mistakes evidently continued to bother Marsh, as he wrote in his last letter to Henry Woodward, some ten years later, regarding some casts he was sending him: "...considering what confusion there seems to be in your country on the subject [of the Dinosauria], good casts of the characteristic American specimens might help on the missionary work of scientific instruction, and thus aid in bringing still nearer together our two countries." (Woodward 1899). Although Hulke was in the wrong in his identification of those particular flat bones, he was at least partly in the right, as the other bones that he used in his description (not associated with the large flat plate-like bones) are still regarded as belonging to the stegosaurid *Lexovisaurus* (Hoffstetter 1957).

At the time of Marsh's visit, Arthur Smith Woodward was a relatively new employee at the British Museum (Natural History) (Townsend 1962), who specialised in fossil fish. Alerted to the piscine nature of this specimen, Smith Woodward gave early intimation in a review of the fossil record of sturgeons that a new fish was soon to be described, stating his belief that it was a large "Acipenseroid" (Smith Woodward 1889a). However, the anticipated description was somewhat disappointing when it emerged in print (Smith Woodward 1889b). Certainly, the reported sizes of the bones were impressively large, but their identifications were extremely vague and uncertain (Smith Woodward 1889b), Smith Woodward later admitting that beyond the gill rakers and fin-rays, the true identities of the bones of this fish were still far from clear (Leeds & Smith Woodward 1897).

Unsatisfactory though Smith Woodward's initial description of Alfred Leeds' specimens (the type BMNH P.6921 and the "doubtfully associated" BMNH P.6922) might have been, it did also note that the remains of this fish had also been found in the Callovian Vaches Noire of Normandie in France – specimen BMNH 32581 (fig. 4.2) (Smith Woodward 1889b). In spite of this, Wenz omitted *Leedsichthys* from her 1967 faunal list of fossil fish that occurred in the Vaches Noire area between Villers-sur-Mer and Houlgate, mentioning only *Mesturus* and *Eurycormus* (Wenz 1967). The distribution of *Leedsichthys* was clearly not restricted to the district of Peterborough, and indeed a 265mm long fin-ray fragment of *Leedsichthys* excavated from the Oxford Clay of Christian Malford (fig. 4.1), Wiltshire, had already been purchased by the British Museum (Natural History) from William Cunnington Esq. in February 1875 (BMNH 46355).

4.4 - FRENCH FINDS

The specimen from Vaches Noire (Dives, Normandie) noted by Smith Woodward (1889b) is a concretion 12cm across, containing around twenty disarticulated gill rakers ranging in length from 98-114mm (fig. 4.2). It was purchased by Richard Owen as part of "a series of specimens from the Jurassic of Normandie" from "M'sieu Tesson of Caen" in 1857, recorded as "Branchiostegous rays of Fish" (Palaeontology Department specimen catalogues, additions Geology, Vertebrata volume 2; NHM unnumbered; Buffetaut 1983), and is the earliest known collected specimen of *Leedsichthys*. There has been a thriving culture of fossil collectors in the area between Villers-sur-Mer (fig. 4.1) and Houlgate for many years, to the extent that Flaubert referred to it in his posthumously-published novel 'Bouvard et Pécuchet' (Flaubert 1884) (noting, in the process, the reputation that the collectors of Villers had, of selling their specimens to the English). In this novel, the two main characters are retired, and develop an enthusiasm for collecting fossils. Almost prophetically, at one point Bouvard and Pécuchet believe that they have discovered a gigantic fossil fish in the Jurassic cliffs of Normandie (albeit at the Bajocian type locality of Falaise des Hachettes), but it is so fragile that they destroy it while attempting to retrieve it.

The tradition of private collectors on these beaches has continued to the present day: Bardet *et al.* (1993) used material collected recently by M & M Charles and G & E Pennettier for her histological analysis, which identified fossilised remains as belonging to *Leedsichthys*, and the Pennettiers still acquire well-preserved material (including *Leedsichthys*) from this site (pers. obs.). The Callovian outcrop at this locality today is

extremely poor. In the late nineteenth and early twentieth century, the ledges of Upper Callovian would usually become visible in the winter, but this has become rarer. At the start of the twentieth century, nearby excavations for a dam and local railway resulted in the sand level rising to cover the *Peltoceras athleta* zone. The situation has slowly deteriorated over the decades since then: collectors today have to dig below the 0.5-1 metre thick sand at the foot of the Kimmeridgian-Toarcian Vaches Noire cliffs at low tide, under the constant threat of the imminent return of the tide. The fossil material yielded reveals not only the presence of *Leedsichthys*, but also a Callovian assemblage of pliosaurids, plesiosaurids and crocodilians, as diverse as that of the Oxford Clay around Peterborough. Although problematic to access, in many ways the material has advantages over the English equivalents, as it is usually well supported by internal sediment and so preserved in three dimensions (figs. 4.3-4.5), rather than crushed flat (figs. 4.6, 4.7). Some specimens occur in nodules, requiring hours of mechanical preparation, but the results are greatly enlightening in terms of the overall morphology of the undistorted bones.

In 2004 a new *Leedsichthys* locality (fig. 4.9) was discovered in the Argiles d'Ecqueville supérieur north of Octeville at Cap de la Hève (fig. 4.1), northeast of the Villers-sur-Mer Vaches Noire Callovian locality (D. Gielen, pers. comm., 03/2005). This is particularly important as it is an Upper Kimmeridgian occurrence (Gallois 2005), and extends the stratigraphic range of this genus by 5 million years. The Kimmeridge Clay of Dorset was referred to as a source of *Leedsichthys* material by Arthur Smith Woodward (Smith Woodward 1895; Leeds & Smith Woodward 1897; Zittel 1925) but with no record of where the relevant specimen(s) might have been deposited. No material matches this description within the collections of the Natural History Museum (London). It has been suggested (Martill, pers. comm.) that climatic change at the end of the Callovian (Dromart *et al.* 2003a, 2003b) was responsible for driving *Leedsichthys* from the northern hemisphere via the Hispanic Corridor (Riccardi 1991; Whatley & Ballent 1994; Tethys Seaway of Arratia 1996) so that after the Callovian the genus continued only in the southern hemisphere (see 'American Occurrences', below). However, it is clear from this occurrence in the Upper Kimmeridgian of France that if this constraint was in effect, then it was only a temporary restriction of the geographical range of *Leedsichthys*.

4.5 - 'SCHWANZSTACHELN'

In 1901 Friedrich von Huene, of the University of Tübingen, Germany, visited the Woodwardian (now the Sedgwick) Museum of the University of Cambridge, to review possible dinosaur material held in the Cambridge collections (Huene 1901). Following this

visit, he published on a number of the specimens in the collection that he had interpreted as dinosaur material. Amongst these specimens was a series of associated bones that he figured as 'schwanzstacheln', or tail spines, of a stegosaurian dinosaur (specimen number CAMSM J.46873; fig. 4.10). The bones had been collected in 1899 by Henry Keeping, a rival collector to Alfred Leeds. Alfred Leeds had an arrangement with many of the quarrymen excavating the Oxford Clay in the pits around Peterborough, whereby he would financially reward them for notifying him of any bones they came across (Leeds 1956). In order to get the quarrymen to give bones to him instead of Leeds, Keeping resorted to telling them that Leeds had stopped collecting bones (which he had not - Alfred Leeds continued to collect and prepare bones up until his death in 1917) (Leeds 1956). Keeping had acquired the material examined by von Huene (1901) from clay brick pits in the Fletton district south of Peterborough – Alfred Leeds' prime collecting ground. Leeds was alerted to the erroneous identification by his friend Bernhard Stürtz of Bonn, who sent him a copy of von Huene's paper (1901). Leeds commented on the misidentification in a letter to Arthur Smith Woodward the same year, saying "I should like to have a cut at old Keeping – so as to expose his ignorance in putting these bones together – but it does not look as though any one at Cambridge knew much about bones." (Leeds 1901).

The bones figured by von Huene (1901) are elongate and curved, extend up to a metre in length, and have a 'woven' surface texture common to many bones of *Leedsichthys*, in contrast to the conical and smooth-surfaced tail spines of a stegosaurian dinosaur (fig. 8.20a). In this specimen, through the hardening of the clay matrix into a concretion, something of the *in vivo* relationships of these bones seems to have been preserved (as noted by Huene [1901]). The bones have grooves down their basal lengths, so that they loosely interlink to form a longitudinal base. This sequence of curved elongate elements strongly suggests skeletal components of a meristic series. Possible candidates for such a series in the skeleton of an osteichthyan would be branchiostegals, supraneurals, neural spines, pleural ribs, haemal spines and dorsal fin-rays. Typically there are between thirty and fifty filiform branchiostegals in pachycormids (McAllister 1968), and the bones figured by von Huene are neither the correct shape nor present in large enough numbers for these to be likely branchiostegals. Although it is possible that these elements are supraneurals, their curvature runs counter to that seen in other pachycormids, travelling superiorly then posteriorly, as opposed to posteriorly then superiorly (Smith Woodward 1916; Hauff & Hauff 1981), making these unlikely to be homologous bones to supraneurals. It seems unlikely that pleural ribs would articulate together, and the relatively swift change in curvature and length of these bones over the distance represented

by CAMSM J.46873 would seem to argue against their being ribs or haemal spines, as they would seem to define a shorter fish like *Mola*, unlikely to be combined with such an extensive lunate tail as BMNH P.10000. Although different to the dorsal fin-rays of many osteichthyans, these bones are similar to the unsegmented form seen in other pachycormids such as *Asthenocormus* and *Saurostomus* (Smith Woodward 1916, also specimen JM SOS 3556 which has a fracture running between the two sets of hemitrichia).

Hoffstetter (1957) correctly noted that the bulk of the specimens figured by von Huene (1901: fig.3) were of a giant fish, rather than a stegosaur (Hoffstetter 1957: page 542). Unfortunately Galton (1985), in relaying Hoffstetter's 1957 correction to von Huene's misidentification, referred to these bones as gill rakers. Contra Galton (1985), they resemble the dorsal fin spines (rather than metre long gill rakers) of pachycormids like *Asthenocormus* (pers. obs.) from the Tithonian Solnhofen limestone and *Saurostomus* from the Toarcian Holzmaden shale. A similar view was espoused by Alfred Leeds in a personal letter to Arthur Smith Woodward (The Official Archives of The Natural History Museum, held by the General Library (NHM-GL) and Earth Science Library (NHM-ESL); Alfred Nicholson Leeds to Arthur Smith Woodward, 18 March 1898; Correspondence section NHM-GL DF 100/31(Liston & Noè 2004)). Also, many specimens of *Leedsichthys* contain this type of elongate and curved bone (GLAHM V3363, PETMG F1, PETMG F174, PETMG R189, OUMNH J.1803, NMW 19.96.G9, CAMSM X.50111, CAMSM X.50117, CAMSM J.27444, CAMSM J.46876-8, LEICT G471.1897, LEICT G472.1897, LEICT G473.1897, LEICT G519.1993.1-7, BMNH P.6921, BMNH P.6924, BMNH P.6925, BMNH P.6928, BMNH P.11825, BMNH P.66341, BMNH P.66342), although rarely do they contain such an apparently complete sequence as that represented by the Cambridge specimen.

The other specimens figured and described by von Huene in his 1901 paper on dinosaur material from the Woodwardian (now Sedgwick) Museum did actually constitute stegosaurian and other dinosaur remains. But such mistakes have been common since *Leedsichthys* was first described. Specimens sold to Liverpool University in April 1919 by the Leeds Family as *Leedsichthys* were later erroneously described as bones from the skull roof of the ichthyosaur *Ophthalmosaurus icenicus* and ribs from indeterminate reptiles (Neaverson 1935, see also Appendix IX for further details). Lack of awareness of this fish and the nature of its remains have also frequently led to misidentifications of some of the more obscure remains of other animals, as being components of *Leedsichthys*. In one case, the misidentification of some small actinopterygian jaw bones as the gill rakers of

Leedsichthys led to this fish erroneously being reported as occurring in the Kellaways Sands of Lincolnshire (Brown 1990; Brown & Keen 1991). In another case, a beautifully complete specimen of a pliosaur exoccipital-opisthotic was misidentified as (presumably) being a vertebra of *Leedsichthys* (Noè *et al.* 2003, Appendix VIII), although due to reduced ossification of its skeleton (Liston 2004a), no vertebra has ever been recovered for *Leedsichthys*. This is a phenomenon that varies widely across the Pachycormidae, from the centra being well preserved in a small genus like *Haasichthys* from the Toarcian of Luxembourg (Delsate 1999), to the centra being utterly absent in large Toarcian specimens of *Saurostomus* (Smith Woodward 1916) and *Ohmdenia* (Hauff 1953; Lambers 1992). The preservation of vertebral components can also be seen to vary widely even across different species of the genus *Pachycormus*, excavated from the Toarcian of Holzmaden (Hauff & Hauff 1981).

4.6 - GERMAN OCCURRENCES

Almost a century after the first description of *Leedsichthys*, the geographical distribution of this taxon expanded, with a specimen found in northern Germany, in the Störmer quarry of Wallücke (fig. 4.11), in the 300 metre high chain of the Wiehen Mountains ('Wiehengebirge') between Osnabrück and Minden, near Bünde. In 1978, a school-age group of amateur palaeontologists from the Scientific Club for Bielefeld and District (Naturwissenschaftlicher Verein für Bielefeld und Umgegend), collecting ammonites (fig. 4.13), found the first bony remains from this site – pliosaur bones lying just below the *Erymnoceras* sp. layer that they were collecting from. Over time, as they collected more of these ammonites from the Middle-Upper Callovian strata of the 'Ornatenton' (as the Oxford Clay is referred to in this region), more of the bone-bearing layer was exposed, until in July 1982 the first remains of *Leedsichthys* were recovered. In the same month, another school-age group of collectors, from the Bünde Palaeontological Working Group (Paläontologische Arbeitsgruppe Bünde) independently found the remains of the same fish at the site. But it would not be until six months later that a chance encounter between members of each group (Ralf Metzdorf of the former, and Matthias Metz of the latter) in an entirely different quarry led to the realisation that each group had been excavating the same animal.

In the meantime, the Bielefeld group had brought their finds, resembling fossilised reeds, to Martin Büchner of the Bielefeld Natural History Museum for identification. Although he could not say to what animal they might have belonged, he believed them to be vertebrate and therefore potentially important, and so arranged for them to be passed to the

Office for the Protection of Monuments. The representative from the Office, Mr Niemier, decided that they were fossil plant, and sent Mr. Schultka of the Palaeobotany Research Group of the Westfalian Wilhelms-University to the quarry to collect a sample for analysis. Büchner and Schultka independently thin-sectioned the material and confirmed the original analysis – that it was indeed bone, and not plant material, as Haversian systems appeared to run through it, but no phloem or xylem vessels (fig. 4.14, 4.15).

Following the chance meeting of Metz and Metzdorf, and the results of the histological analysis, a joint excavation was planned by both groups of collectors, running from November 1st to 3rd 1983 (fig. 4.12). This yielded a large number of vertebrate remains (which mainly were transferred to the Westphalisches Museum für Naturkunde, although some pieces entered private collections), spread over an area roughly 30 metres by 30 metres. As a result of this, three further digs were conducted on the same site between 1985 and 1989 by the Westphalisches Museum für Naturkunde, each unfortunately only yielding relatively few remains in comparison with the November 1983 excavation. The last of the three digs reported only finding "a few bone splinters of the previous skeleton...badly eroded by weathering." (Probst & Windolf, 1993: p.157). The vertebrate remains from all of these digs were almost entirely *Leedsichthys*, the only exceptions being pliosaur material and chondrichthyan teeth. Importantly, this Störmer specimen was the first to ever be mapped (Probst & Windolf 1993; Michelis *et al.* 1996), albeit retrospectively, by Metzdorf, using photographs taken over almost fifteen years. This provided the first indications of the relative disposition of the bones of a specimen of *Leedsichthys*, as all previously collected specimens had either been accessioned as isolated and unconnected slabs, or had had all matrix removed from them.

In 1986, Metzdorf prepared some of the material in the Westphalisches Museum für Naturkunde and took samples to Dr Rupert Wild of Stuttgart Natural History Museum, who identified one bone (WMfN PM 17006/8) found in the centre of the *Leedsichthys* assemblage as the 'schwanzstacheln' or tail spine of a stegosaurian dinosaur (fig. 4.16). This was despite the fact that WMfN PM 17006/8 is a form of bone that is commonly found in other specimens of *Leedsichthys* from Peterborough (pers. obs.) (GLAHM V3363 (fig. 4.17), PETMG F2, PETMG F174, PETMG R189, NMW 19.96.G8, CAMSM X.50118, CAMSM J.27438, CAMSM J.67471, LEICT G418.1956.15.2, LEICT G418.1956.15.5, BMNH P.6921, BMNH P.11823), and possesses a different surface texture, cross-section and no taper, compared with a stegosaurian tail spine (fig. 4.19).

It should be emphasised that this is a completely different element to the bone misidentified by von Huene as a 'schwanzstacheln' some 80 years earlier (Huene 1901). The tail spines of *Lexovisaurus* are three dimensional solid cones, with an extremely smooth external surface, whereas WMfN PM 17006/8 is hollowed and commonly presents as crushed in other specimens of *Leedsichthys*. This bone is a hypobranchial, from the anterior part of the gill basket of *Leedsichthys*. As well as the crushed material listed above, this identification can be confirmed by comparison with the uncrushed hypobranchials present in the articulated gill basket specimen BMNH P.10156. This identification was supported during the June 2002 excavation of the most complete specimen of *Leedsichthys* (PETMG F174) yet found, jointly organised by the University of Portsmouth and the University of Glasgow's Hunterian Museum (see Appendix VII/Liston 2006). The initial identification of the possible presence of a specimen of *Leedsichthys* in the brick pit near Peterborough was made through a fragment of a bone that was a mirror image of one of the dorsal fin-rays figured by von Huene as 'schwanzstacheln'. After more than ten weeks of digging, consisting of 3,119 hours of fieldwork, more than 2,100 bones from the specimen (nicknamed 'Ariston', because it went 'on and on') had been retrieved. Amongst them was the bone morphotype identified at the Wallücke site as being a *Lexovisaurus* 'schwanzstachel', medial to the body end of a pectoral fin (fig. 4.18), in the midst of other branchial elements and a dense mass of gill rakers. The Wallücke hypobranchial (WMfN PM 17006/8) is still displayed in the Westphalisches Museum für Naturkunde under the incorrect description of *Lexovisaurus* 'schwanzstachel'.

The misidentification of the isolated bone as stegosaurian was unfortunately consolidated in print by the publication of the results of a Masters Project in 1996 (Michelis *et al.* 1996), which also created new levels of confusion by attempting to set out a histological means of distinguishing between the 'stegosaurian' bone and the bones of *Leedsichthys*, and proceeding to thus formally amend the diagnosis of the taxon. The bulk of the *Leedsichthys* bone morphologies retrieved from Wallücke are highly fragmented branchial arch elements and caudal fin-rays. One piece, WMfN PM 17006/1 (incorrectly figured in Michelis *et al.* (1996) as WMfN PM 17005/1 in Abb.5 the 'find-plan' map; in addition, WMfN PM 17005/2 is incorrectly noted in Michelis *et al.* (1996) as WMfN PM 17006/1 in Plate 2 Figure g), is a 470mm long section of fin-rays that appear to exceptionally show tendons linking parallel rays (fig. 4.20). Apart from small fragments, the only significant dermal skull material is represented by WMfN PM 17005/23 (fig. 4.21) and WMfN PM 17005/24 (fig. 4.22). These two pieces are part and counterpart, with what appears to be a skull roof bone on WMfN PM 17005/23 impacted on to parts of the opercular series on

WMfN PM 17005/24 (fig. 4.23). Another bone of interest is specimen number PHB W 138/4 (Breitkreutz private collection): in a similar error to Galton (1985), Michelis *et al.* (1996) notes this as a gill raker, and illustrates it with a scale bar indicating a total size of around 75mm. In actuality, this is incorrect as the illustrated specimen is in fact 310mm long (the scale bar is incorrectly noted at 25mm, when it is actually 100mm), and not a gill raker, but a fragment of a left cleithrum. Although this specimen (fig. 4.24) is similar to the 480mm long object figured in Abb.12 (PMM 19.1-21.1, 23.1 (fig. 4.25)), it is likely that this latter object is a component of the lower jaw, possibly the supraangular, although a final identification has not proved possible. The same element is represented in BMNH P.66340 (which features the only dentary of *Leedsichthys* known) and the ventral gill basket specimen (BMNH P.10156/3). The fact that this element is only found with these two specimens (which predominantly represent the skeleton of the lower jaw area), and that only the dentary is known from the lower jaw ramus, is why it is suggested that this bone is a lower jaw element. It is worth noting that in the absence of any gill rakers with the Wallücke specimen, these elements with the fin-ray fragments are the only osteological link between these fossil remains and other specimens of *Leedsichthys*.

Although the description of much of the material from this quarry was correct, the spurious allocation of a bone to *Lexovisaurus* was indeed wrong – and having so correctly identified the rest of the bones, it is hard to understand why this morphology was allocated to a dinosaur completely unknown from the locality. Fragments of this German specimen of *Leedsichthys* are still cropping out today at the same site (pers. obs.). In 2002, pieces were collected (GLAHM 109518) and sampled for growth ring information, from which an estimated age of seventeen years, and a standard length estimate of around 7 metres have been derived (for methods, see Chapter 7). The remains of *Leedsichthys* have also been reported from the same stratigraphic level in a neighbouring quarry in the Wiehengebirge – Luttersche Egge (pers. comm. Metzdorf). But the Wallücke specimen itself, through a combination of different independent collecting activities and protracted weathering out over a number of years from a 40 degree inclined 900 square metre area, has become spread throughout a series of different public, as well as private, collections.

4.7 - EVIDENCE FOR OTHER POSSIBLE EUROPEAN OCCURRENCES

Although no hard fossils of *Leedsichthys* have been identified in Central Europe, some Callovian age 'Rinnen' or 'gutter' traces uncovered in the Liesbergmüli clay pit (fig. 4.1, 20 km SW of Basel, Switzerland) in 1987 have been interpreted as 'feeding troughs' formed by large marine vertebrates preying on invertebrates inhabiting *Rhizocorallium*

surface burrows (fig. 4.26) in less than ten metres water depth (Geister 1998). Geister interpreted the largest (in terms of both length and width) of these (figs. 4.27, 4.28) as being produced by pliosaurs, a conclusion rejected by Noè (2001) on the grounds that it would be physically impossible for a pliosaur to manoeuvre its head to generate the troughs without breaking its neck.

Geister specifically dismissed *Leedsichthys* as a potential manufacturer of these furrows, on the grounds that it was a filter feeder, but this is far from an obstacle. Geister proposed *Lepidotes*, *Asteracanthus* and *Heterodontus* as possible candidates for creating the narrower traces, arguing that there was a requirement for any candidate to have durophagous (crushing) dentition, but there are contemporary models for this type of feeding behaviour without such teeth. The recent *Heterodontus* can pump water and sand across its gills in order to expose prey hidden in the surface of the seabed. The recent freshwater fish, the Siberian sturgeon (*Acipenser baeri*), ingests large amounts of sediment and detritus while feeding on its benthic prey (chironomid larvae, amphipods, isopods and polychaetes) (Sokolov & Vasil'ev 1989). Traces of such invertebrate fauna are commonly found in Callovian and Oxfordian marine sediments (e.g. Radwańska 2004). Although previously the paddlefish has been cited as a 'benthic siever' in this style, Grande and Bemis (1991) have recently questioned whether this behaviour has actually been observed, or simply assumed from the unusual cranial morphology of these bony fish. Jobling (1995) also alludes to pleuronectids employing 'suctorial feeding' on benthic prey, but does not indicate the degree to which sediment is taken into the mouth, or further ingested by the body, during this process. Another recent suspension feeding fish *Abramis brama* (van den Berg *et al.* 1992) derives 50% of its nutrition from zooplankton extracted from the water column through suspension feeding with its well-developed gill raker system, and 50% from chironomid larvae on the bottom of the lakes that it inhabits, although it bears edentulous jaws.

There are also marine, if non-piscine, examples of similar iliophagous behaviour, which are more comparable in terms of the size of the predator involved in extracting invertebrate prey from the surface sediment of the sea bottom. Murray *et al.* (2002) reviewed the largescale impact of such activities by a range of vertebrates. Hans Nelson and Johnson (Hans Nelson & Johnson 1987; Hans Nelson *et al.* 1987) have noted the production of channels similar to Geister's 'feeding troughs' in seafloor sediments at depths of 30-50 metres by California grey whales and Pacific walruses. The furrows created by Pacific walruses (*Odobenus rosmarus divergens*) are the results of the walrus hydraulically

clearing the mud from clams detected in the sediment with its vibrissae. The walrus then sucks the clam from its shell. In contrast, the California gray whale (*Eschrichtius robustus*) feeds by sucking in large quantities of sediment containing the tube mat of the amphipod crustacean *Ampelisa macrocephalus*, which it then separates from the surrounding sediment, using its baleen plates. Like *Abramis brama*, the California gray whale also feeds on organisms that live in the water column. Although neither is a precise model for a trough generated by the predator's head ploughing a furrow in the sea bed, as Geister interprets the Liesberg traces, they establish the precedent of large marine vertebrates taking mouthfuls of fauna-rich sediment from the sea floor, in order to extract epibenthic invertebrates for ingestion, in a manner capable of generating large-scale feeding trails. It can be envisaged that this might be a form of feeding that a fish would grow into, through ontogenetic changes altering its range of prey and feeding styles (Jobling 1995) in the same way as the feeding habits of any fish change with growth, as the feeding structures within the mouth attain an effective size to deal with extraction of prey from sediment.

So, far from being unreasonable for a suspension feeding animal to generate these troughs, there are plenty of contemporary examples of a wide range of suspension-feeding vertebrates indulging in this behaviour. Given the quantity of marine vertebrates today that can facultatively utilise this benthic food source, it would be surprising if such a vertebrate did not occur in the Callovian marine ecosystem. There is nothing in the anatomy of *Leedsichthys* to contraindicate such a feeding strategy, and van den Berg *et al.* (1994b) specifically suggested that interdigitating gill rakers of the form displayed by *Leedsichthys* indicates a facultative suspension feeder that could vary its interraker gap in order to change its diet from benthic to suspension feeding and back again. It may have been that feeding on benthic invertebrates was the preferred feeding strategy for *Leedsichthys* when a suitably rich source of plankton was not immediately available. Geister's (1998) argument that these troughs are biologically generated is convincing, the troughs are wide, the margins smooth, orientation meandering (like those formed by Pacific walruses on the Bering Shelf, Hans Nelson & Johnson 1987) or straight. Reviewing the recognised Callovian marine fauna, and excluding the pliosaurs on the biomechanical grounds suggested by Noè (2001), leaves *Leedsichthys* as the only currently known candidate to have a gape large enough (up to 600mm in width) to generate such a trough in the fashion suggested. These widest troughs (Geister's gutter-type 'c') are also the ones that can exhibit a sinusoidal trough pattern (rather than the straight lines of the other gutter traces), perhaps reflecting the regular lateral oscillation of a swimming body travelling in

anguilliform or carangiform mode (Blake 1983), rather than random movements or foraging behaviour. But this is all at best circumstantial evidence, and in the absence of any body fossils to support arguments for the presence of this fish in this environment, this model remains conjecture.

The marine Callovian outcrops further east in Europe, noteably in Poland and south-east of Moscow, but thus far no report of *Leedsichthys* has been made from these regions. A 70mm-diameter fish vertebra has been reported from Poland's marine Callovian (A. Radwanski, pers. comm. 2004), but as no vertebrae have ever been identified from *Leedsichthys*, this find is unlikely to belong to that fish. As noted before, *Leedsichthys*, like some other members of the Family Pachycormidae, appears to exhibit a trend towards non-ossification of this part of its skeleton. As such, this vertebra is more likely to belong to a large example of a caturid like *Osteorachis* (known from the Peterborough Oxford Clay; Martill 1991) than to *Leedsichthys*.

4.8 - REMAINS FROM THE AMERICAS

In terms of sedimentary marine units that might represent an appropriate environment for an animal such as *Leedsichthys*, the North American Sundance Formation seems a likely candidate. The Callovian-Oxfordian range of the Formation (Uhlir *et al.* 1988; Weems & Blodgett 1996) neatly encompasses the range of the fish, as described earlier. Although parts of the formation represent a shallower environment than the Oxford Clay (Uhlir *et al.* 1988), it has proven to be a deep enough marine environment to be a source for large marine vertebrate remains (Knight 1898; Weems & Blodgett 1996). As such, it might be considered surprising that the remains of *Leedsichthys* have not yet been identified within this Formation, but it has been argued that the marine reptiles occurring in the Sundance Formation exhibit an apparent provincialism that indicates a possible discrete Late Jurassic biogeographic Boreal Realm (Weems & Blodgett 1996). If this reflects a geographic or environmental separation between the Middle-Upper Jurassic European and western North American assemblages, then it would not be surprising for this constraint to also have applied to a large fish such as *Leedsichthys*.

However, the remains of *Leedsichthys* are not simply constrained to Europe: although the Jurassic of North America has not yet yielded any remains, the Jurassic (Oxfordian, 157.1-154.7mya) of South America has. Alexander Andrew Fergusson Leeds (or 'Fergie' as his family called him), the eldest son of Alfred Leeds (the original discoverer of *Leedsichthys*), worked for the copper miners Norman Walker & Co. in Antofagasta in Chile (fig. 4.29)

from 1897 until 1903. By a somewhat bizarre coincidence, in August 1978 in the archaeological museum of this same city on the western edge of the Atacama Desert, Hans-Peter Schultze (of Lawrence University) came across the remains of a large fish (figs. 4.30, 4.31) from the local Middle Jurassic. Brought into the Museo de Arqueologia over the previous five years, the remains seemed to represent extremely large gill rakers within a limestone matrix. Although, like Arthur Smith Woodward's first provisional identification, they were marked as possibly being part of a large acipenseroid/chondrostean fish (Smith Woodward 1889a), they were in fact the remains of *Leedsichthys* (Arratia & Schultze 1999). On chancing upon them in the Museo de Arqueologia, Antofagasta, Hans-Peter Schultze organised a dig, which retrieved more *Leedsichthys* material from Quebrada San Pedro and Quebrada Aquada Chica for this museum (fig. 4.32). In March 1994 at a nearby locality north of Quebrada del Profeta, he discovered and excavated a new and extensive specimen embedded in an extremely large block of limestone matrix (fig. 4.33) (Arratia & Schultze 1999) over several days with pickaxes and shovels. Like the other Atacama material, this specimen preserves detail well, but the remains are less robust than the matrix surrounding it, making preparation difficult. The Quebrada del Profeta 1994 material (Museo Nacional de Historia Natural, Santiago) is preserved in nodules, and has yet to be fully prepared for analysis. Its extensive nature (filling several crates) indicates a specimen that has much valuable information to contribute about the anatomy and lifestyle of this remarkable animal, in particular the structure of its gill basket. Shortly after this excavation, Martill and Frey were presented with a specimen of what was thought to be an accumulation of *Pterodaustro* mandibles (fig. 4.34). The sample had been retrieved during an annual student trip from a site some 190-200 miles north of the Schultze excavation area (fig. 4.35) (Martill *et al.* 1999; Liston 2004a). The block was recognised as a lump of *Leedsichthys* gill rakers, but with what appeared to be fenestrae along the length of the ramus (Martill *et al.* 1999). These 'fenestrae' were used as the basis of erecting a new species of *Leedsichthys*, namely *Leedsichthys notocetes*, but subsequent analysis has revealed that these features actually appear to be erosional artefacts (Steel, pers. comm; see Chapter 6).

4.9 - SUMMARY

It is interesting to contrast the perhaps understandable repeated confusion of the pachycormid *Leedsichthys* with a large acipenseroid fish (given the prominent gill rakers and branching finrays common to both) with the somewhat bizarre confusion between three utterly different bones of *Leedsichthys* and a stegosaurian dinosaur (other specimens

of *Leedsichthys* have been misidentified as stegosaurian within the Sedgwick Museum's collections, but these have not been formally published). It emphasises the need for general awareness to be raised regarding the appearance and form of the remains of this remarkable animal.

4.10 - CONCLUSIONS

An account has been given of the geographical and stratigraphical extent of *Leedsichthys*. Misidentifications have been addressed, with particular emphasis on the dorsal fin-rays and the hypobranchial element of the gill basket.

Chapter 5

"rather aberrant pachycormiformes"

Brian Gardiner, 1967

Chaper 5:

A Review Of The Characters Of The Edentulous Pachycormiforms *Leedsichthys*, *Asthenocormus* And *Martillichthys* (nov. gen.).

5.1 - ABSTRACT

With their phyletic trend of non-ossification of their skeleton, the members of the Mesozoic neopterygian Family Pachycormidae have long presented problems to systematists. Recent works on this family are revisited with additional data for *Leedsichthys*, *Asthenocormus* and *Martillichthys* (nov. gen.) from the Callovian Oxford Clay around Peterborough (UK). A revised diagnosis of the Family Pachycormidae is presented, along with an updated strict consensus tree for the Pachycormiformes, showing the edentulous pachycormiforms as a discrete clade.

5.2 - INTRODUCTION

The Pachycormidae were an extensive family of Mesozoic neopterygians, ranging in adult size from 300 mm (Delsate 1999) to 8900 mm (see Chapter 7), and extending from the Toarcian to the Campanian (Lambers 1992).

Patterson (1982) has noted that Smith Woodward (1891) first used the term Actinopterygii to describe the chondrosteans, holosteans and teleosts as a natural group of fishes, based on Cope's 1871 grouping of Actinopteri, and has speculated that this was prompted by his 1889 work on fossil sturgeons. It seems likely that the more specific catalyst for Smith Woodward's assessment that this was a natural group of fishes, was alluded to in the reference within his fossil sturgeons survey to there being traces of a new very large fish from the Oxford Clay, with stiff branched rays and irregular dermal bones that made it very 'Acipenseroid'-like (Smith Woodward 1889a). This was the first mention of the fish that Smith Woodward would later the same year describe as *Leedsichthys problematicus* (1889b), a name that he would soon attempt to change (to the *nomen novum* of *Leedsia problematica* 1890b), despite having already published the original name a further three times beforehand (Smith Woodward 1889c, 1890a, Smith Woodward & Sherborn 1890). It is significant that when, in the following year (January 1891), Smith Woodward published the section of the British Museum Fossil Fishes Catalogue that dealt with the 'acipenseroid' fishes (Volume 2, Smith Woodward 1891), that this fish was not mentioned, and when the subsequent volume (3, Smith Woodward 1895) emerged in 1895 he classified it as part of the new Family Pachycormidae. It appears likely that changing his

original assessment of this particular fossil from his SubOrder Chondrostei to his SubOrder Protospondyli had focussed Smith Woodward's mind on the similarities as well as the differences between these two broad groups. This publication was also the first that referred to a Family Pachycormidae. Since then, both Actinopterygii and Pachycormidae have become established terms, although there have been differences of opinion as to where the latter sat within the former (e.g. see Patterson 1973 and Arratia & Lambers 1996, Arratia 1999 for Pachycormiformes as either primitive teleosts or non-teleosts).

The aim of the current work is to describe the pachycormid specimen BMNH P.61563 in order to assess the identification of *Asthenocormus* sp. given to it by Schaeffer & Patterson (1984). To aid in the interpretation of aspects of its branchial structure, the gill basket of *Leedsichthys problematicus* (BMNH P.10156) will also be described. The results of these studies will form the basis of a phylogenetic analysis of the Pachycormidae, following on from Lambers' (1992) work.

5.3 - MATERIALS AND METHODS

Three major assessments of the relationships within the Pachycormidae have been conducted since Smith Woodward defined the Family (1895): Wenz (1967, covering 3 genera) and Mainwaring (1978, covering 6 genera) primarily focussed on the genus *Pachycormus* for their work, but Lambers (1992, covering 11 genera) worked on the wider group, although largely ignoring *Leedsichthys* (of the 16 characters that he used for examining interrelationships within the Family Pachycormidae, only 2 characters are completed in his dataset for this genus). It is his dataset that will form the foundation of the current work. As well as adding a further 9 characters to the dataset for *Leedsichthys*, and making some minor corrections to the dataset for other taxa, a new genus is introduced to his character matrix.

MATERIAL REVIEWED FROM THE FOLLOWING INSTITUTIONS

The specimens examined belong to the Dresden Museum (Ba), Dresden, Germany; Natural History Museum (BMNH), London, England; Hunterian Museum (GLAHM), University of Glasgow, Glasgow, Scotland; Jura-Museum (JM), Eichstätt, Germany; Peterborough City Museum (PETMG), Peterborough, England; Musée national d'Histoire naturelle de Luxembourg (Tu), Luxembourg.

The following taxa were studied:

Asthenocormus sp. - BMNH P.61563.

Asthenocormus titanius. - BaJ2344; JM SOS 542; JM SOS 3556.

Haasichthys michelsi. - Tu228.

Leedsichthys problematicus. - BMNH P.6921; BMNH P.10000; BMNH P.10156; GLAHM V3363; PETMG F174.

Pachycormus macropterus. – GLAHM V7274.

Pachycormid, unidentified. - PETMG F161.

5.4 - MORPHOLOGICAL DESCRIPTION

5.4.1 - Description of specimen BMNH P.61563

The specimen to be described is a 2110 mm (SL, equals standard length, *sensu* Holčik *et al.* 1989, 2305 mm = total length) fish recovered from the Oxford Clay of the Dogsthorpe Pit (fig. 5.1) of the London Brick Co., Peterborough, in summer 1983. The variation between standard and total length comes in part from shear that has slightly displaced the cranium relative to the lower jaw, and in part from the twisting of the caudal lobes, that has rendered accurate estimation of the posterior extent of the tail of this specimen impossible. This twisting of the lobes may also be obscuring the position of the hypural plate, if it was indeed preserved.

As removed from approximately 70 mm above the base of Bed 12 (Hudson & Martill 1994, Martill 1986a) of the Dogsthorpe Pit, the specimen is made up of a series of fourteen slabs of clay in addition to the block containing the skull. The specimen conforms to Martill's (1986a) interpretation of a fish that has lain flat on the sea bed, stabilised by long (relative to body height) pectoral fins, suffering some dorso-ventral compaction. The specimen is utterly devoid of scales, with no teeth present in any of the skull components. The skull has been chemically prepared so that it is utterly free of matrix and exists as a three dimensional flattened skull, extensively consolidated with Paraloid B72. The right pectoral fin (contained within Blocks 3 and 4) has been mechanically prepared and embedded in foam to support it (fig. 5.2A) – the base of the left pectoral fin on Block 4 has also been prepared (revealing what is likely to be the nearby right pelvic fin as well as showing small fish vertebrae, identified by Martill as *Leptolepis* sp. [1986a], within a black organic mass that may represent foregut contents), but the rest of this fin is still embedded in Blocks 5 and 6. Block 10 has been prepared to show the anal fin (fig. 5.2B), the most posterior ray of which is situated 570 mm from the caudal peduncle. The fin has a base that extends for 17 mm and a length of 91 mm. The remains of the dorsal fin is visible on Block 11 (fig. 5.2B). It has a base extending for 47 mm and although damage prevents determination of its full original extent, its remains indicate a length of more than 49 mm. Its most posterior ray is situated 730 mm from the caudal peduncle. Ribs mark the outline

of the body cavity (fig. 5.2B) in Blocks 6-14 inclusive, tapering from a maximum width of 100 mm across Block 6 to 35 mm around the caudal peduncle in Block 14. Block 14 also contains the mechanically prepared and consolidated caudal lobes (fig. 5.2C). The preparation work on the select components present in blocks 3, 4, 10 and 14 means that they, like the skull, now only approximately connect with the nine unprepared slabs.

The following descriptions of skull material follows the terminology based on homologisation of skull roof bones in osteichthyans (Westoll 1943).

5.4.1.1 - Skull, dorsal view (fig. 5.3A, B)**:** Although some damage to the skull has resulted from compression as well as shear, the skull bones have tended to retain their sutured connections, only fracturing around the orbit and opercular regions. The skull roof is preserved clearly with unusually extended parietals anteriorly meeting the posterior border of the rostrodermethmoid. The suture is structurally supported and strengthened by a series of fibrous cross-sutural 'struts'. The rostrodermethmoid continues forward to meet the posterior borders of both nasals (bones noted by Lambers [1992] as being absent in *Asthenocormus*), and is thus excluded from the anterior border of the skull. Both nasals have sustained some damage, with only parts of both antorbitals still present, occupying part of the lateral borders of the nasals. No premaxillae are present, and both mandibles form the lateral border of this block, extending from anterior to the nasals, posteriorly to half of the length of the parietals. The post-parietals at the rear of the skull are flanked by the dermopterotics, and a fracture runs through the anterior region of these four bones, dividing the skull into two pieces. Posterior to these bones, the skull roof gives way to the left and right exoccipitals surrounding a 6 mm foramen magnum, and the exposed blade-like epibranchials beyond.

5.4.1.2 - Skull, ventral view (fig. 5.4A, B)**:** The lower jaws lie separated at the symphysis, each ramus made up of three blade-like unfused bones – this does not appear to be an artefact from preservational compression or torsion, as the separations are clear. Anteriorly, these are the dentary, articular and prearticular, posteriorly these are the angular, articular and prearticular. Laterally, both maxillae are visible at the outer edges of the dentaries. Flanking the ceratohyals are the bones of the lower jaw joint, the surangular and angular articulating with the quadrate. Posterior to the left quadrate, the left symplectic, interopercle and subopercle are clearly displayed. One result of the shear that the skull has been subjected to is the removal of parts of the left preopercle and opercle. The unusually elongated ceratohyals (233 mm, with an 18 mm maximum dorsoventral

depth) sit behind a fragment of a paired gular and the exposed anterior portion of the parasphenoid, along with over 27 diverging branchiostegal rays. This first set extends 53 mm down the length of the paired hypohyals and the anterior ceratohyal, before running a further 30 mm down the posterior ceratohyal. A second set of converging branchiostegals then runs for the remaining 157 mm, straddling the inter-ceratohyal gap to the posterior end of the posterior ceratohyals. The ceratobranchials emerge from deep to the ceratohyals, and like the epibranchials are thin, elongate and blade-like.

5.4.1.3 - Postcranial general description: The lack of preservation of any component of the vertebral centra, combined with the limited preparation of the specimen, the large quantity of consolidant (that often prevents accurate observation) present and the 'stacking' of the pleural ribs renders even an estimated count of the number of meristic units impossible without significant further preparatory work.

5.4.2 - COMPARISON WITH OTHER EDENTULOUS PACHYCORMIDS

As an edentulous pachycormid, this animal automatically attracts comparisons with the other two edentulous pachycormids, namely *Leedsichthys* and *Asthenocormus*. The remains of these two genera are very different – one genus is known from three or four poorly prepared complete specimens, the other is known from a large quantity of isolated cranial and postcranial material, virtually none of which is articulated, presenting very particular problems of identification (Aldridge 1986, Liston 2005). This means that there are very few characteristics that can be evenly compared across all three taxa. As such, a different approach will be employed for comparing each genus with specimen BMNH P.61563.

BMNH P.61563 was initially identified (Schaeffer & Patterson 1984) as *Asthenocormus* sp., an identification later echoed by Martill (1991: p.220-222), so it is necessary to compare BMNH P.61563 with the type material of *Asthenocormus*. Lambers (1992) noted that the type specimen of Wagner (1863) in München was lost, as was Vetter's 1881 specimen in Dresden. In the absence of complete specimens that were already described in the literature, Lambers selected Jura-Museum specimen JM SOS 542 as a neotype, and provided a description of it, supported by the complete specimen JM SOS 3556 and other private collection material. Since then, the counterpart of Vetter's Dresden specimen (BaJ 2344) has recently resurfaced in the Dresden collections (pers. obs., fig. 5.6). The somewhat diminutive length of that specimen (1176 mm against the SLs of the two Jura-Museum specimens of 1920 mm and 2100 mm, and the recorded length of the original type

specimen as 2335 mm [Wagner 1863]) raises the possibility that it might prove to be a subadult or juvenile individual, and therefore adds further support to Lambers' choice of one of the large Jura-Museum individuals as a neotype. As well as containing apparent gut contents (like BMNH P.61563, and similar to evidence found while excavating *Leedsichthys* PETMG F.174, pers. obs.), and a three dimensionally preserved section of the gastrointestinal tract similar to the valvular intestine of *Megachasma pelagios* (Taylor *et al.* 1983) the megamouth shark (but see also Eastman [1914] re different interpretation in a specimen of *Hypsocormus*), the Dresden specimen has also helped to retrospectively inform Lambers' initial character analysis (see below), particularly with respect to Vetter's report of the presence of an anal fin in the genus (1881). One of the particularly useful things about the two Jura-Museum specimens, is that they are both very close in size (SL of 1920 mm and 2100 mm) to BMNH P.61563 (SL of 2110 mm), so any observed differences in relative proportions of elements of the skeleton are not likely to result from differences caused by allometric growth.

The lower jaw of BMNH P.61563 seems very different from *Asthenocormus* (or indeed any of the other taxa in the Family Pachycormidae). The lower jaws of all three *Asthenocormus* specimens are fairly well exposed, and can be compared with the completely exposed lower jaw of BMNH P.61563. BMNH P.61563 has a ratio of maximum height of dentary/length of lower jaw of 1:7.33. Both adult *Asthenocormus* specimens have far lower ratios of 1:4.24 and 1:4.47. The skulls of *Asthenocormus* also occupy a far greater proportion of their standard body length (1:3.03 and 1:3.62) than BMNH P.61563 (1:4.67).

The pectoral fin of BMNH P.61563 is classically 'pachycormid' – scythe-like and curved. The pectoral fins of *Asthenocormus*, in contrast, are more falcate, projecting out from the body like a tied bundle of sticks. This is also true for its dorsal fins, with a short fin-base relative to the length of the fin. As the number of rays in the fin of a bony fish becomes fixed during embryological development (although the number of segments/articulations and bifurcations will usually change with age), it seems that the fin-rays appear to present a basis for character definition. As observed by Arratia & Lambers (1996) the tails of pachycormiform fishes are noteworthy as the dorsal and ventral elements are virtually symmetrical with respect to the body axis, and this means that damage to one caudal lobe will not prevent the number of its fin-rays being estimated, provided that the other lobe is intact and can be examined.

For all three *Asthenocormus* specimens, the number of rays in each caudal lobe was 28-30. In BMNH P.61563, the ray count in each lobe averaged 44. For the pectoral fins, the ray count for the three *Asthenocormus* specimens was in the range 14-18. The ray count for the prepared pectoral fin of BMNH P.61563 was 26 rays.

In only two of the three *Asthenocormus* specimens was the dorsal fin prepared adequately enough for a count of the rays to be possible, and they gave totals of 40 and 44. The ray count for the partially-prepared dorsal fin of BMNH P.61563 was 25 rays.

As first noted by Martill (1991), BMNH P.61563 appears to have a pelvic fin just beneath and behind the prepared pectoral fin. This could be some separated rays from the pectoral, but the sudden change in size of rays makes it seem more likely that this is indeed a pelvic fin. The presence of pelvic fins in *Asthenocormus* is unlikely. Lambers (1992) noted that none have been recorded by any author, but if they were of a similar size and in a similar position to the pelvics of BMNH P.61563, then they would indeed be difficult to distinguish from the hard to discern white pectorals against the white Tithonian Solnhofen limestone (pers. obs.).

Lambers (1992) also recorded Wagner's observation (1863) of the original holotype that there was no anal fin present, but that Vetter (1881) reported a small anal fin on the Dresden specimen. Referring to the surviving counterpart of this specimen (BaJ 2344), a small (73 mm long fin base) anal fin is indeed apparent, originating 791 mm behind the tip of the skull, beyond the level of the posterior extent of the dorsal fin. Although difficult to detect on the neotype specimen (JM SOS 542), the anal fin is a discernible if largely unexcavated feature on the other Jura-Museum specimen (JM SOS 3556), situated 1349 mm behind the tip of the skull, with a 96 mm long base to the fin. As has been noted, the length of the anal fin base in BMNH P.61563 is 17 mm.

It may be an artefact of BMNH P.61563 being dorsoventrally rather than laterally preserved (see Martill 1986b), but the absence of vertebral centra in this specimen appears to leave a transverse gap between each pair of ribs that is significantly larger than in either *Asthenocormus* or *Saurostomus* (both genera have vertebral centra that fail to preserve, presumably due to non-ossification). A difference that probably has more to do with the vagaries of preservation between the Oxford Clay and the Solnhofen limestone, is that impressions of the centra in *Asthenocormus* are preserved, which can be used to determine a vertebral count, but no such impressions are recorded in the Oxford Clay of BMNH

P.61563. As previously noted, the stacking of the ribs in this specimen also inhibits an assessment of how many body segments this animal would have had.

In spite of the undisturbed nature of the remains of this fish, no hypural plate is present in this specimen, although a possible ?preural vertebra is present (Fig. 5.2C). Although the tail is twisted and this complicates interpretation, it seems less like the extreme thunniform/semilunate character of *Asthenocormus* and far more like that of *Pachycormus macropterus* (e.g. GLAHM V7274) and *Leedsichthys* (BMNH P.10000).

5.4.2.1 - Comparison of skull roofs: A clearer comparison of the two taxa (*Asthenocormus* and *Leedsichthys*) with the specimen under consideration (BMNH P.61563) is possible through comparison of the skull roofs (fig. 5.5).

Although some damage has occurred to the dermopterotics and the specimen is not fully prepared, it can be seen that in *Leedsichthys* a large boss is present at the posterior margin of the parietals and dermopterotics, and a well-defined 'notch' is formed at the anterior margin of the parietals. In the neotype of *Asthenocormus*, no such notch or postparietal boss is present, and the dermopterotics have extremely accentuated posterior and anterior angles, extending significantly beyond the rear of the postparietals and forward along the lateral border of the parietals. In BMNH P.61563, there is no such forward sweep in the dermopterotics, and the backward sweep of the posterior angle is far more modest, barely extending past the postparietal posterior tip. The dermopterotics in BMNH P.61563 form the lateral borders of the postparietals in a way that they do not in *Leedsichthys*. As in *Leedsichthys*, there is an indentation on the anterolateral border of the parietals (absent in *Asthenocormus*), but there is an additional posterolateral indentation for the parietals of BMNH P.61563. The posterolateral indentation approximates the position of the maxilla, the anterolateral indentation occurs at the expected position of the premaxilla (the premaxilla is unknown in both *Leedsichthys* and this specimen). But there is no trace of the fracturing on *Leedsichthys* that would be expected if it had a similarly tightly-"knitted" parietal-rostrodermethmoid suture, as specimen BMNH P.61563 shows. Bearing in mind that the *Leedsichthys* skull roof (918 mm long) is more than four times the length of the skull roof of BMNH P.61563 (212 mm long), were this latter specimen in fact a juvenile *Leedsichthys* one might expect that with increased growth the suture would be strengthened in both appearance and structure, rather than weakened. Also, the width/length ratio of the parietals for *Leedsichthys* is 1:1.63, with the parietals forming 60.5% of the parietal/postparietal length, whereas the width/length ratio for the parietals in

Asthenocormus is 1:2.34, with the parietals forming 80.7% of the parietal/postparietal length. These latter values are very close to the values of 1:2.31 and 76.4% for specimen BMNH P.61563, indicating that even although the morphology of these bones is significantly different, their relative growth is very similar between this specimen and the neotype of *Asthenocormus*.

5.4.2.2 - The gill -basket of *Leedsichthys* (BMNH P.10156) (figs. 5.7, 5.8-5.11):
Knowledge of the gill basket of *Leedsichthys* is based primarily on a single specimen sold by the collector Alfred Leeds to the British Museum of Natural History on the 22nd July 1905 (as part of a batch of material bought for £150, see Liston & Noè 2004). It consists of several isolated slabs of clay containing lengths of fin-rays (probably pectoral, pers. obs.), a hyomandibula of 870 mm length, and the bulk of an articulated gill basket with some opercular elements. Owing to its preservation within a concretionary nodule, virtually all the elements excepting the hyomandibula and the fin-rays can be placed in their original unexcavated positions, and indeed the bulk of this latter material made up a single display item in the fossil fish gallery of the British Museum from 1905 (Bather 1923, 1936) until 1987 (fig. 5.7).

Following recent extensive and careful consolidation work by the Palaeontological Conservation Unit of the NHM (London), it is possible to reconstruct the gill basket as it was originally found, and examine both sides, for the first time since 1905 (fig. 5.8-5.11). This is important, because an earlier published sketch of this specimen (Martill 1988) misinterpreted the one displayed surface (the ventral aspect) as showing fusion of the first three branchial arches. This is in fact an artefact of excavation, whereby a large amount of the matrix has been left in place in order to hold the left hypobranchials and the anterior ends of the left ceratobranchials in place, and this matrix has partially been obscured by the fragmentary remains of the left ceratohyal overlying this area.

The gill basket consists of both hypohyals, a left hypobranchial I, both hypobranchial IIs, both 810 mm long ceratobranchial Is, both 950 mm long ceratobranchial IIs, both 990 mm long ceratobranchial IIIs, both 940 mm long ceratobranchial IVs, and the 340 mm long basibranchial IV. Combined with the fused arch V, they produce a gill basket 1140 mm wide and 1545 mm long (Liston 2005). The ceratobranchials are elongate prisms with a robust isoscelean right-angled triangular cross-section that is normally flattened through compression during preservation in other specimens (see Chapter 4 and section 8.3.1.4). The hypobranchials are discrete from the ceratobranchials, and the change in angle at their

junction of 21.5 degrees would seem to indicate a lower branchial arch joint, which is associated with fish with an exceptionally wide gape (Yasuda 1960).

The removal of the matrix (with any possible associated gill rakers) from much of the two extended elements lying posterolateral to the left I ceratobranchial make it unclear whether or not this is in fact part of the left I upper arch (sensu Yasuda 1960 = epibranchial plus pharyngobranchial), and indeed this is the only evidence for what the epibranchials of *Leedsichthys* may have looked like. The abduction angle (sensu van den Berg *et al.* 1994b) of the gill basket is around 15.5 degrees at the junction between the basibranchial and the fourth ceratobranchial.

5.4.2.3 - The gill -basket of BMNH P.61563 (figs. 5.3, 5.4): As the currently known specimens of *Asthenocormus* are preserved in lateral rather than dorsal or ventral views, comparative information is not available for the gill basket of this taxon. However, specimen BMNH P.61563 has parts of its gill basket conspicuously exposed on its dorsal and ventral surfaces. Dorsally, four paired epibranchials are visible posterior to the rear of the skull roof (although the right epibranchials are overlain by the right opercle, their topology is still visible). They occupy an area 83 mm across, the central epibranchials reaching 80 mm in length, and a depth of at least (in the case of the left epibranchial III) 9 mm. On the ventral surface, the five paired ceratobranchials form a gill basket 50 mm wide and 128 mm long, the longest visible element (ceratobranchial I) being 93 mm long, and at least 4 mm deep (although these elements may extend further, deep to the symplectic and both ceratohyals). An abduction angle of between 6.5 and 7 degrees is visible at the junction between the basibranchial and the fourth ceratobranchial. Apart from the significant difference in arch angle, the most striking difference between the gill basket of this specimen and that of *Leedsichthys* is that the ceratobranchials are thin and blade-like medio-laterally, and do not at all resemble the robust branchial elements with triangular cross-section present in *Leedsichthys*. Clusters of 'tooth'-like objects lie loosely in the matrix at the posterior ends of the 5th ceratobranchials, on the right epibranchial I and the left epibranchial III and IV. They range in size from 1.5 to up to 4 mm long. Given their scattered, scarce, isolated and unlocated nature, it seems more likely that they come from scavengers rather than belonging to the animal itself (fig. 5.12).

Broader works (Nelson 1969) that have attempted to assess the gill basket form of larger groups of actinopterygians do not indicate more about *Leedsichthys* and specimen BMNH P.61563 than that they conform to the general holostean type. Similarly, McAllister (1968)

looked at the broader relatedness of 'teleostome' fishes through comparison of their branchiostegal apparatus. No branchiostegals have yet been described for *Leedsichthys* (although Smith Woodward included elements suggested to be branchiostegals in his original description [1889], he later [1895] stated that he thought it more likely that they were "vertebral arches" – see section 8.3.1.7). There is some damage to the branchiostegals on specimen BMNH P.61563, but it is clear that they are spathiform and that there are over 27 present on each side, which is within the 6+/- 50 range of McAllister (1968) for Pachycormiformes, and close to the 30-50 that McAllister describes as typically pachycormiform.

Conclusions from examination of specimen: Initially identified as *Asthenocormus* sp. (Anonymous 1984, Schaeffer & Patterson 1984, Martill 1985; 1991), it has also been suggested that BMNH P.61563 represents a juvenile example of *Leedsichthys* (Martill, pers. comm. 1999-2004). However, there are a number of characteristics that distinguish BMNH P.61563 from both these genera. The preceding analysis indicates that not only is specimen BMNH P.61563 a member of the Family Pachycormidae, but it is also distinctive enough from all other members of the group not simply to be a new species, but to warrant its own distinct genus. As such, it is proposed to erect a new genus based on this specimen.

5.5 - SYSTEMATIC PALAEONTOLOGY

Class Osteichthyes HUXLEY 1880

Sub-Class Actinopterygii COPE 1887

Division Halecostomi (sensu PATTERSON 1973)

Order Pachycormiformes

Family Pachycormidae WOODWARD 1895

***Martillichthys renwickae*, nov. gen et nov. sp.**

Synonymy:

1984 *Asthenocormus* sp. SCHAEFFER & PATTERSON p.74-75

Etymology: Refers to David Michael Martill, the finder and excavator of the specimen, and his co-worker Gillian Hazel Renwick, in recognition of their services to fossil collecting from the Oxford Clay.

Type material: Holotype - BMNH P.61563, a complete specimen with flattened three dimensionally preserved skull.

Referred Material – PETMG F.161, a largely unprepared specimen in a concretionary nodule, extending from the anterior tip of the skull to the posterior part of the base of the pectoral/pelvic fins. Also referrable is PETMG F175, a completely unprepared circa 2 metre long individual situated on the surface of a concretionary nodule, consisting of skull, dorsal and caudal fin material.

Diagnosis: A pachycormid with the following autapomorphies: rostrodermethmoid occluded from the tip of the snout, so excluded from the anterodorsal border of the mouth; absence of teeth, scales, segmentation of the fin-rays, vertebrae, and hypural plate; a fin-ray ratio of 40-48 caudal rays, 21-26 dorsals and 21-26 pectoral rays; lower jaw articulation within the horizontal range of the orbit; highly elongate and unfused mandibular elements; skull length/standard length ratio of 1:5.5-6.5; highly elongated gill basket, extending beyond rear of skull roof.

5.5.1 - Phylogenetic analysis

In order to quantify the degree of difference represented by BMNH P.61563, Lambers' (1992) dataset showing the distribution of derived character states within Pachycormidae will be expanded to include this specimen, and some character states previously recorded for other taxa will be reassessed.

Characters 1-15: Distribution of derived character states within the Pachycormidae. The first two characters of Lambers concern the rostrodermethmoid. In *Leedsichthys*, a rostrodermethmoid is yet to be identified. The rostrodermethmoid in *Martillichthys* does not reach the tip of the snout or the lower jaw symphysis, and appears to be edentulous.

Characters 3 and 4 concern the premaxillary dentition, and the premaxilla has not been identified for either genus (*Leedsichthys* or *Martillichthys*).

Characters 5 and 6 concern the dentary dentition, and the dentary appears to be edentulous in both genera (*Leedsichthys* and *Martillichthys*).

Character 7 relates to the presence of needle teeth on gill rakers. They can be found on gill rakers of *Leedsichthys* (but note Chapter 6), and associated structures have been identified as rakers with teeth for a specimen of *Asthenocormus*, but they are absent from the gill rakers found on *Martillichthys* (fig. 5.12). This is a character that can only be easily assessed in the larger representatives of the Pachycormidae, where the rakers can readily

be seen and examined, and even then the needle teeth may not be preserved if incompletely ossified (van den Berg *et al.* 1994c). As such, the presence/absence of these 'needle teeth' is a character that cannot be rigorously demonstrated for smaller representatives of the Family (e.g. *Sauropsis*, *Haasichthys*). Furthermore, as loss of teeth (state 2 of characters 2, 4, 5 and 6 of Lambers' dataset) and proliferation of gill rakers are characteristics that frequently go together (Nelson 1967, Sanderson & Wassersug 1990, Lazzarro 1987) and that the presence of secondary structures such as gill raker needle teeth have frequently been reported with such gill raker proliferation (e.g. Peck 1893, Yasuda 1960, de Ciochomski 1967, Friedland 1985, Gibson 1988) this may be a form of repeatedly coding for the same suite of characters, giving the transition undue weight. It is therefore suggested that character 7 be deleted from the dataset.

Character 8 relates to the presence of a boss at the rear of the skull roof, which is absent in *Martillichthys*, but present as a postparietal structure in *Leedsichthys*.

Characters 9-13 relate to fins. Character 9 refers to the relative placement and origin of the dorsal and anal fins, which cannot be determined in *Leedsichthys*, but can in *Asthenocormus* and *Martillichthys*. Although it seems clear on the basis of fin size which fin lies most anteriorly on the body of BMNH P.61563, there is some twisting to the body and damage to the fins. Characters 10 and 11 relate to the presence of a pelvic fin and pelvic plate – there is no evidence for any pelvic structures in *Leedsichthys*, and although a pelvic plate is not visible in *Martillichthys*, the right pelvic fin appears to be present. Character 12 relates to the shape of the anal fin, which in *Asthenocormus* and *Martillichthys* is triangular. In *Leedsichthys*, although the anal fin is not fully preserved, several anal fin proximal fin supports along with individual rays are, allowing it to be reconstructed as triangular. Character 13 relates to caudal fin-ray segmentation/articulation, which none of the edentulous Pachycormiformes display.

Character 14 relates to the presence of either a double or a single row of supra neurals between the skull and the dorsal fin – although *Asthenocormus* and *Martillichthys* do not display a double row, remains of *Leedsichthys* indicate the presence of this character.

Character 15 relates to the ossification of vertebral centra, which none of the edentulous Pachycormiformes display. In spite of this, specimens of *Asthenocormus* leave impressions that make it possible to count the vertebral centra in its axial skeleton, but this is more of a feature of the exceptional preservational qualities of the Solnhofen limestone

compared with the Oxford Clay, than of any intrinsic difference in ossification of chordacentra.

Incorporating this information into Lambers' data matrix (Table 5.1), an unordered character analysis was run to assess where the new taxon might sit in relation to Lambers' consensus tree (Lambers 1992: fig. 23, p. 281).

5.6 - RESULTS OF THE PHYLOGENETIC ANALYSIS

Using PAUP v4b10 (Swofford 2002) to run an unordered analysis of the 15 intra-pachycormid characters including *Martillichthys* produced the following strict consensus of 46 trees (fig. 5.13). The addition of this taxon does not destabilise any clades generated in Lambers' consensus tree, but it also fails to resolve the tetrachotomy at node B of *Sauropsis*, *Euthynotus*, (*'H. macrodon'* + *Orthocormus* + *Protosphyraena* + *Hypsocormus insignis*) and *Pseudoasthenocormus*. The resolved dichotomy under Lambers changes from (*Saurostomus* + *Pachycormus*) as the sister group to (*Asthenocormus* and *Leedsichthys*), to (*Saurostomus* + *Pachycormus*) as sister group to (*Martillichthys* + (*Asthenocormus* + *Leedsichthys*)) at node C.

Node B is supported by the character of the falcate anal fin (Character 12), and node C by the linked characters of the pelvic fin (Characters 10 and 11). More characters are clearly required in order to not only resolve the tetrachotomy of node B, but to add support to C.

Comparing these results to Mainwaring's (1978) is difficult, as half of the taxa used here are not included in her analysis (e.g. none of the edentulous Pachycormiformes are utilised), and Lambers revised her character definitions before applying them himself (1992), but her analysis did produce the dichotomy of (*Saurostomus* + *Pachycormus*). When Lambers added *Orthocormus* to her dataset (1988), the two dichotomies of (*Saurostomus* + *Pachycormus*) and (*Orthocormus* + *Protosphyraena*) were present, with (*Hypsocormus* + (*Orthocormus* + *Protosphyraena*)) emerging as the sister group to (*Saurostomus* + *Pachycormus*).

5.6.1 - Definition Of The Pachycormidae On The Basis Of Derived Characters

The characters identified by Lambers for definition of the Pachycormidae on the basis of derived characters were not used in the above analysis, which was focussed on the interrelationships within this group. However, some points do arise in connection with these characters that should be noted for further work.

Lambers' (1992) 16 characters to define the Pachycormidae have some apparent weaknesses in relation to the edentulous members of the group. Although *Asthenocormus* shows particularly pachycormid uroneural characteristics, the necessary bony elements do not preserve or are not present in either *Leedsichthys* or *Martillichthys*. Neither are any scales preserved in these three taxa. This would seem to reflect the overall trend within the Family Pachycormidae towards increased non-ossification throughout the skeleton.

Characters 16-18 relate to the role of the rostrodermethmoid in the skull. In *Martillichthys* the nasals exclude the edentulous rostrodermethmoid from the anterior extremity of the skull, so that all three characters score against the pachycormid state. In *Asthenocormus* the nasals are not preserved, and in *Leedsichthys* neither the nasals nor the rostrodermethmoid have been identified.

Similar issues arise with characters 19 and 21 – the supramaxilla and premaxilla are absent/not identified in all specimens of all three genera.

Characters 20 and 22 relate to the lower jaw, the coronoid process of which is not visible in *Martillichthys* and the articulation of which is within the horizontal extent of the orbit. Like *Asthenocormus*, the orbit of *Martillichthys* is situated dorsal to the posterior part of the maxilla, rather than the anterior part of the maxilla as in other pachycormids.

Given that Lambers' (1992) characters 17, 18, 22, 29, 30, 31 have been demonstrated not to hold true for all pachycormids, the Family Pachycormidae are defined as a group by the presence of the following synapomorphies: anterior part of skull roof formed by median rostrodermethmoid (Character 16); supramaxilla posterodorsal to maxilla (Character 19); lower jaw with low coronoid process (Character 20); dorsal border of lower jaw with an elevation opposite to the premaxilla (Character 21); at least six infraorbitals behind orbit (Character 23); infraorbitals at posteroventral corner of orbit not expanded posteriorly, with one infraorbital situated below the orbit (Character 24); dermosphenotic forms dorsal border of orbit (Character 25); two large plate-like posteriorly expanded suborbitals (Character 26); pectoral fin scythe-like, fin-rays only segmented distally (Character 27); pectoral fin-rays bifurcating asymmetrically in a 'y'-shaped fashion (Character 28).

5.7 - CONCLUSIONS AND DISCUSSION

A new genus is described from the Oxford Clay (Callovian) of Peterborough, and a revision of Lambers' (1992) analysis of the Pachycormidae presented, incorporating new and revised data from *Leedsichthys* and *Asthenocormus*. The results of Lambers' (1992) analysis are supported, with the edentulous Pachycormiformes emerging as a discrete clade. A revised diagnosis of the Family Pachycormidae is presented.

Work to further resolve the interrelationships of the rest of the members of the Pachycormidae is outwith the scope of the immediate project, but could perhaps be progressed by analysis of fin-ray numbers and degree of axial skeleton ossification across the taxa. Clarification of the position of *Martillichthys* would be aided by further preparation of the axial skeleton of BMNH P.61563, as well as full preparation of the skull and pectoral fins of the suspected second specimen of this genus, PETMG F161. It is hoped that the future incorporation of other pachycormid genera described since Lambers' analysis (e.g. Delsate 1999, Blanco-Piñón *et al.* 2002) will also help clarify the evolution of this remarkably successful group of fishes.

Chapter 6

"The principal function of the gill-rakers is to protect the delicate filaments - as one might conclude from the law of action and reaction. It is only secondarily that they are connected with the food. The 'selection' of the latter depends on the senses, and a fish, we may be sure, does not trouble to consult the gill-rakers when it is hungry."

Harry Kyle, 1926

Chapter 6

Phylogenetic Burden and the Gill Raker – Buckling under the Strain?

6.1 - ABSTRACT

Pachycormids represent part of the first radiation of the total group of teleosts, and therefore are important in understanding stem teleost phylogeny. Gill rakers (or *fanunculi*) are elements of the gill skeleton (branchial basket) in fish, that function primarily to protect respiratory lamellae, and sometimes have a secondary role in feeding. Characteristics of gill rakers have been used for taxonomic diagnosis and cladistic analysis of the interrelationships of Pachycormiformes, with particular importance for *Leedsichthys* and *Asthenocormus*. The material on which these determinations have been based is reviewed, along with the validity of use of gill rakers in analysis of extinct fish in general, based on their utility in extant fish. The interrelationships of Pachycormiformes are then reanalysed, following the work of Lambers (1992). Gill rakers are demonstrated to be an unreliable source of taxonomic characters. The assignation of PETMG F34 to *Leedsichthys* is questionable, but its dissimilarity to other specimens identified as *Leedsichthys* may be due to its subadult nature. The validity of *Leedsichthys notocetes* as a distinct species from *Leedsichthys problematicus* is called into question, as the primary distinction between the two appears based on an artefact structure generated by erosion and fracture.

6.2 - INTRODUCTION

Pachycormids are a poorly understood group of Mesozoic actinopterygians that represent part of the first radiation of the total group of teleosts (Arratia 1999), and therefore are important in understanding stem teleost phylogeny. Of all the taxa in the Family Pachycormidae, the most poorly known is the enigmatic Callovian-Kimmeridgian genus *Leedsichthys*. When Arthur Smith Woodward named the taxon *Leedsichthys problematicus* (1889b), he was fully aware that it was a difficult taxon to describe. Found amongst the vertebrate material collected from the Oxford Clay by Alfred Leeds, some of its bones had already been published under the misidentification of stegosaur armour (Hulke 1887). Since Smith Woodward's description of the Peterborough and Normandie Oxford Clay material, different elements of its remains have been published as belonging to a stegosaurian dinosaur on a further two occasions, and it has been misidentified as fossil plant material on another (see Chapter 4). Conversely, some of the more obscure bones of other taxa (e.g. pliosaurs, Noè *et al.* 2003) have also been attributed to it as a form of Oxford Clay 'wastebasket taxon' for vertebrate remains that were uncommon or unusual. *Leedsichthys* material sold to Liverpool University in April 1919 by the Leeds

Family was later erroneously reidentified as ophthalmosaur and 'reptilia indet' (Neaverson 1935). The recurrent pattern of a complete lack of understanding of the osteology of this animal has three underlying causes: firstly, the large (but indefinite) size of the animal has made interpretation of the remains difficult; secondly, these remains are most commonly crushed flat and broken into fragments, disguising their true *in vivo* shape and size; thirdly the remains are invariably partial (often simply consisting of a few isolated elements) and do not represent an entire individual. All three of these causes are at least partly the result of the reduced ossification prevalent throughout *Leedsichthys* skeleton. This set of problems with the material (isolated, disarticulated, scattered, fragmentary, disjunct) has meant that, in spite of its size, this animal has had a similar set of barriers obstructing the understanding of its nature, to those surrounding conodont animals (Aldridge 1986).

Although initially described in 1889, it was not until 1895 that Arthur Smith Woodward declared that *Leedsichthys* was not related to the sturgeons or 'acipenseroids' (as he had previously stated, Smith Woodward 1889a,b), but was a member of the Family Pachycormidae (Smith Woodward 1895). It is perhaps, therefore, of little surprise that following Smith Woodward's attempt to shorten the name he had designated for the fish (introducing the *nomen nudum* of *Leedsia problematica* – despite having already published the original name four times himself in Smith Woodward 1889b, 1889c, 1890a; Smith Woodward & Sherborn 1890), it was fully ninety eight years before another attempt was made to revisit the description or taxonomy of this animal. Martill (1988) amended Smith Woodward's diagnosis to state that it was a "fish of gigantic proportions", and noting dimensions relating to gill rakers, the gill basket, the caudal fins and an unretrieved ?pectoral fin-ray. The use of absolute size in a diagnosis is rarely helpful, as (provided the specimen upon which the description is based can be determined to be an adult) it hinders the identification of sub-adult and juvenile material, and makes it difficult to distinguish between convergence and synapomorphy. Although knowledge that *Leedsichthys* was able to grow to a given size (and the estimated size of the fish has been a matter of some debate, with estimates ranging from 9 metres (Smith Woodward 1917, and see also Liston & Noè 2004) to over 27 metres (Martill 1986a)) is of use for understanding an animal's ecology, statements of relative or proportional lengths are of more universal utility in matters of diagnosis.

Eight years after Martill published his modification to Smith Woodward, Michelis *et al.* (1996) amended Martill's revised diagnosis on the grounds of the histology of material found in the Callovian Oxford Clay or 'Ornatenton' of northern Germany. The concept of

histology as having a diagnostic role within fossil fish material has a long history (e.g. see Enlow & Brown 1956 for a review). Michelis *et al.* (1996) examined some of the material from the north German specimen of *Leedsichthys*, noting the presence of very fine blood vessels running parallel to the external bone surface and the 'absence of a *compacta*'. They then sought to demonstrate that *Leedsichthys* could be distinguished from 'higher' vertebrates and diagnosed on the basis of these characters. However, Ricqlès *et al.* (1991) specifically noted that 'peculiarities' of bone histology cannot be regarded as being taxa-specific evidence with taxonomic significance, and Francillon-Vieillot *et al.* (1990) expressly stated that the presence or absence of *compacta* is not diagnostic of precise anatomical or ontogenetic origins (Francillon-Vieillot *et al.* 1990). This dismissal of that means of diagnosis was also inadvertently validated by Michelis *et al.* themselves, as they went on to misdiagnose a hypobranchial of *Leedsichthys* as a tail-spine of a stegosaurian dinosaur, using their *compacta*-based methodology to rule the element out from being a part of the *Leedsichthys* skeleton (1996). Compact bone is present in *Leedsichthys*, albeit in a very much reduced thickness for the comparatively large size of the bones concerned (fig. 7.14). This is a reflection of the reduced ossification of the skeleton that occurs as a phyletic trend across the Pachycormidae – not only have specific elements of the skeleton not ossified at all, but the majority of the rest of the skeleton has only ossified with a very thin superficial layer of compact bone over extensively resorbed and remodelled cancellous bone. This means that the bones of *Leedsichthys* from the Oxford Clay are most commonly preserved crushed and flattened (if not fragmented), unless exceptional preservation (e.g. within a concretion) has occurred. (Noteworthy exceptions that commonly survive relatively uncrushed due to their denser compact bone layer, are the hyomandibulae and the ceratohyals.)

Arthur Smith Woodward's species name of *problematicus* reflected his own uncertainty regarding the identification of the bony remains of *Leedsichthys* – underlined when he wrote some years later (Leeds & Smith Woodward 1897) that of the eight bones that he had identified in his original description, he could only really be certain of the osteological identity of two of them: the gill rakers and the fin-rays (lepidotrichia). Indeed, in the hundred years since the remains of *Leedsichthys* were first noted in the collection of Alfred Nicholson Leeds (Hulke 1887), the only elements of its skeleton to be figured were two fragments of gill rakers from the holotype specimen BMNH P.6921 (Smith Woodward 1890b) (fig. 6.1).

6.2.1 - Broader Relationships

These skeletal problems have similarly obscured the relationships between *Leedsichthys* and other pachycormids. Although a number of studies have featured *Pachycormus* or *Hypsocormus* as representatives within broader Neopterygian or basal teleost relationships (Gardiner *et al.* 1996, Arratia 1999), only two works have ever attempted to deal with the interrelationships of the members of the Family Pachycormidae (although see also Arratia & Lambers 1996). In the first significant cladistic analysis of the pachycormids, Mainwaring (1978) excluded *Leedsichthys* from the Family Pachycormidae, based on a misperception of there being a a very limited diversity of skeletal elements represented in specimens of the taxon. Lambers (1992) reviewed Mainwaring's work, presenting the most recent hypothesis of the interrelationships of the group, and although he brought *Leedsichthys* back into the Family Pachycormidae, he experienced problems in obtaining useful characters for this genus. He presented only two characters for this genus in his final published analysis of the interrelationships of Family Pachycormidae: one of these was fin-ray character (bifurcation without segmentation in the caudal fins), the other was a gill raker character (the presence of 'needle teeth').

Characters that can be used only with significant caution for contemporary fish as a component of a broader suite of characters (e.g. Popper & Coombs 1982), are sometimes successfully used in isolation for fossil taxa (Keller *et al.* 2002, Gaudant 2003). In the light of this, it is worth assessing the stability of gill rakers as biological objects, to determine their robustness and potential suitability for use as a source of diagnostic characters. This is important not just for the use of gill raker characters within and outside the Family Pachycormidae, but also because a second species of *Leedsichthys* has been erected solely on the basis of characteristics apparent in a cluster of disarticulated and isolated gill rakers (*Leedsichthys notocetes* Martill *et al.* 1999).

6.2.2 - The General Form of Gill Rakers in Osteichthyans and Chondrichthyans

Gill rakers (*fanúnculi*) sit as either single or paired structures on the buccal aspect of the branchial arch in osteichthyans and chondrichthyans, sometimes also occurring in modified form within epibranchial organs (Howes 1981, Lazzarro 1987). Their basic form is governed by their primary function, which is to protect the delicate respiratory surfaces of the gill lamellae/filaments from potential damage by particulate matter in the water taken in to the buccal cavity during respiration. They occur in most, but not all fish (Kyle 1926, Magnuson & Heitz 1971), and with varying degrees of distribution throughout the

branchial arches, but the first arch is usually the main site. They have been noted in fossil fish from the Oxford Clay other than *Leedsichthys* (Smith Woodward 1897a, b). Regardless of relative sizes of different elements, the basic structure of a gill raker follows the same general pattern (fig. 6.6):

- A broad **base** (Peirong 1989), which can be bifid, forms the site of insertion for raker abduction muscles (*Interbranchiales abductores* of Winterbottom 1974, *Abductor branchiospinalis* of van den Berg *et al.* 1994a) originating on the branchial arch component.
- From this base, a **stalk** (Kazanski 1964, Peirong 1989) extends from the base into the interarch gap.
- The stalk terminates in the interarch gap as a **tip**.

The stalk may or may not carry accessory/secondary structures on its lateral and medial (e.g. branchiospinules Gibson 1988, Sanderson *et al.* 1996b) or dorsal surfaces ('process' of Yasuda 1960, 'barbs' of Peck 1893, 'denticles' of de Ciochomski 1967, 'branchiospinules' of Friedland 1985, 'teeth' of Gibson 1988). These secondary structures on gill rakers are distinct from the dermal ossifications known as microbranchiospines or microgillrakers, which sit within the epidermis of the gill arch close to its base, and should not be confused with them (Beveridge *et al.* 1988).

The form of gill rakers varies widely across many groups of fishes (Imms 1904). In some fish, their function as a defensive barrier has been refined to include a role in trapping and extracting suspended food particles from the water for ingestion. In a functional sense, their form and frequency has often been correlated to the diet of the respective fish (Nikolsky 1963, Yasuda 1960, Iwai 1964, Helfman *et al.* 1997), with spacing of rakers being regarded as particularly diagnostic in this regard (McNeill Alexander 1967). Hyatt, however, noted (1979) that although fish with closely-spaced gill rakers are plankton feeders and those with coarsely spaced gill rakers are not, fish can still be effective plankton feeders without closely-spaced gill rakers.

For those fish with gill rakers, Van den Berg (1993) suggested that the more comb-like (or 'setiform', Imms 1904) the raker, the more random the orientation of the fish's prey was likely to be. Sanderson *et al.* (1994) similarly noted that the character of the gill raker implied the feeding style of the fish: the thinner and more comb-like the raker (e.g. *Polydon spathula, Cetorhinus maximus* Imms 1904), the lower the buccal flow velocity; the larger the raker, the more it was designed to cope with a higher buccal flow velocity, not by actively retaining prey, but by redirecting current flow to other retention areas (see

also Cheer 1987). In comparing the structure of gill rakers as relating to a planktivorous diet, Jobling (1995) described "fine filamentous gill rakers" being used as traps for prey, and that some fish have a fine enough mesh of gill rakers to not just feed on zooplankton, but smaller phytoplankton as well (e.g. *Engraulis ringens*; *Brevoortia* can collect particles as small as 13-16 microns; some *Tilapia* species can also filter phytoplankton). Ryther (1969) also noted clupeids with specially modified gill rakers for herbivory. Grande & Bemis (1991: page 43) interpreted the diet of an extinct paddlefish on the grounds of the similarity of its gill raker form to particular living paddlefishes.

Although sieving through a comb-like structure has already been alluded to as a means of prey retention for suspension-feeding fish, filtration by mechanical sieve is far from being the only process employed. The exact mechanics of the process is unknown for most fish – for 70 species in 21 families in 12 orders that suspension feed (Cheer *et al.* 2001), Sanderson *et al.* (1996b) noted that there were 56 suspension-feeding fish species in 16 families for which the particle retention mechanism was unknown. Some suspension feeders can feed on small particles without well-developed gill rakers (e.g. *Tilapia melanotheron* feeding on 50-100 micron particles, Hyatt 1979), and others are entirely unaffected in their ability to suspension feed when their gill rakers are surgically removed (e.g. *Sarotherodon galilaeus* tilapia, Sanderson *et al.* 1996b). For those fish for which the process of trapping and extracting suspended food particles from the water for ingestion has been determined, the mechanisms vary widely (Gerking 1994). A functional continuum exists from pure sieving (Bemis *et al.* 1997), to crossflow filtration (Sanderson *et al.* 2001), to trapping and extraction solely through the use of mucus (Goodrich *et al.* 2000). Throughout these mechanisms, the role of the gill raker varies from merely directing water flow (either towards the roof of the mouth, Sanderson *et al.* 1991, or towards the main current flow through the oral cavity, Sanderson *et al.* 1996a), to sieving particles (Sanderson *et al.* 1998), to acting as a crossflow surface (Sanderson *et al.* 2001).

Regardless of mechanism, there is undoubtedly a high correlation between hypertrophy of rakers on gill arches, an increase in their numbers per length of gill arch, and a tendency towards suspension-feeding (Sanderson & Wassersug 1990). Similarly, Lindsey (1981) noted a "convergent suite of planktivore characteristics" in open-water plankton feeders that included high gill raker counts and long gill rakers, that had evolved separately at least three times. This pattern is sometimes additionally accompanied by the occurrence of edentulous jaws, and also by the development of epibranchial organs (an accessory digestive structure located on the roof of the mouth – Takahasi 1957; Nelson 1967, 1970)

at the expense of pharyngeal dentition, and has been noted in five different families of 'lower' teleosts (Sanderson & Wassersug 1993). Lazzarro (1987) interpreted the elaboration of gill rakers as part of a major evolutionary divergence from the basic teleost pattern of generalised predators, towards microphagy. In association with a trend towards replacement of teeth by elaborate gill rakers on branchial arches, he also found changes in the development of protrusibility of the jaws, modification of some gill rakers in an epibranchial organ on the roof of the mouth, and a lengthening of the digestive tract (see also June & Carlson 1971, Bone 1995) to process larger amounts of fine material without the digestive hiatus that is characteristic of macrophages. It is on this basis, that acanthodiforms, with their edentulous jaws and possession of long gill rakers (e.g. *Acanthodes bronni*, in Miles 1973), have been interpreted as microphagous suspension feeders (Janvier 1996, Cech & Moyle 2000). Similarly, the few jaw components that have been identified for *Leedsichthys* are singularly edentulous, and the gill rakers of this fish are of unusually (but not uniquely) large relative size, suggesting that a suspension-feeding lifestyle would be a reasonable model.

6.2.3 - The General Plasticity And Instability Of Gill Rakers – Factors Ephemerally Affecting Gill Raker Morphology

Gill raker form varies greatly throughout the lifetime of an individual fish (June & Carlson 1971, Sanderson & Wassersug 1993), even in terms of whether they are present or absent (Bone 1995). Grande & Bemis, in their landmark review of paddlefishes (SVP Memoir One 1991), noted a niche shift as *Polyodon spathula* grew, with the gradual disappearance of its jaw teeth as its gill rakers developed, and it changed from a carnivore to an edentulous suspension-feeder. Similarly, June & Carlson (1971) noted that the Atlantic menhaden (*Brevoortia tyrannus*) lost all of its teeth as its gill rakers developed, changing from a larval copepod feeder to a juvenile able to filter phytoplankton cells as small as 2 microns. Similar patterns of ontogenetic shift towards gill raker assisted microphagy were also recorded by de Ciochomski (1967). Once a fish has acquired gill rakers, there are still variations in the nature of the gill raker: length varies according to its position on a given gill arch (the longest raker usually being located at the upper arch/lower arch joint Magnuson & Heitz 1971, Gibson 1988, Sanderson *et al.* 1995), and breadth of raker can also vary on a regular basis (Peirong 1989 noting every 3rd-6th gill raker is broad in comparison to the preceding narrow forms in the silver carp *Hypophthalmichthys molitrix*). Kliewer (1970), in reviewing coregonid lake whitefish across a series of lakes, noted that length of gill raker within a species could vary according to the proportion of the diet that was pelagic (longer) or benthic (shorter), in a similar way to the development of

pharyngeal dentition according to available food (Hyatt 1979). He also noted that gill raker length increased with the depth at which the specimen was caught, and that the number of gill rakers per gill arch varied positively with increasing proportions of benthic material in the diet, echoing Lindsey's observation on the variation of gill raker number and length both being dependent on environment as well as age: "gill raker counts expand to fill the available niches." (1981).

Although gill raker numbers and length will generally increase with the age and standard length (SL) of the individual (e.g. *Clupea harengus* Gibson 1988, *Alosa pseudoharengus* MacNeill & Brandt 1990), environmental as well as genetic factors can impinge on the resulting phenotype. Depending on the species, gill raker numbers may increase until the plateau of an 'adult level' has been reached (Villalobos 2002), or they may simply continue to increase in number throughout life (King & Macleod 1976, Gibson 1988, Lindsey 1988). Loy *et al.* (1999) noted the influence of salinity on gill raker number not just during embryonic development, but into adulthood, and stated that gill raker variation might well be ecophenotypic rather than adaptive. The number of gill rakers and their length may also decrease with age and size (e.g. *Seriola* in Sanderson *et al.* 1995).

Hjelm & Johansson (2003) noted that the gill raker spacing in *Rutilus rutilus* responded to environmental change within a five year period, to covary with the size of available zooplankton. Matsumoto & Kohda (2001) similarly noted interraker spacing variations in local populations of *Goniistius zonatus* that appeared to reflect the size of available food at each location. Although the gaps between gill rakers are generally related to food, they can also increase isometrically (*Dorosoma cepedianum* Mummert & Drenner 1986, cyprinids Van den Berg *et al.* 1992), Magnuson & Heitz (1971) even going so far as to present formulae for calculating interraker gaps for standard lengths of given species of scombrids and coryphaenids.

As Loy *et al.* (1999) put it: "The use of gillrakers in systematic studies deserves special attention because variation may not be adaptive but purely ecophenotypic, and environmental conditions may act well beyond the embryo development.". If the parameters of spacing, length, frequency and number of a form are not conserved within the adult life of the animal, how much taxonomic value can they really have?

6.2.4 - Problems Of Historical Use Of Gill Rakers As A Taxonomic Tool

In spite of the above plasticity demonstrated in the characteristics of gill rakers, it should be noted that attempts have nonetheless been made to use them as the basis for taxonomic schemes for some contemporary fish. For example, gill raker number and length have commonly been used as part of a suite of characters to diagnose individual species (e.g. *Bathyclarias* species, Jackson 1959). Yasuda (1960) attempted to establish a scheme to classify Japanese coastal fishes based on their gill raker shape. Iwai established a classificatory scheme based on the histology of taste buds on gill rakers of teleosts (1963, 1964). Kazanski erected a classificatory system for species-level diagnosis of cyprinid fish based on the structure of the gill rakers, even going as far as to develop a pattern of descent, based on characteristics of the gill raker and gill raker cushions (Kazanski 1964). Amundsen (1988) similarly noted Svärdson's use of gill raker number to distinguish between populations of lake whitefish as different species in 1957 and 1979.

6.2.5 - On The Concept Of Needle Teeth

Although used as a character in Lambers' (1992) analysis of the interrelationships of the members of Family Pachycormidae, the presence of 'needle teeth' on the dorsal surface of gill rakers is not a pachycormid synapomorphy. These features occur on the gill rakers of other fish, for example Gibson (1988) referred to it as a feature of the gill rakers of herring, where it is extremely variable in its occurrence, and is not present on the gill rakers of all gill arches. Yasuda (1960) referred to the structures as 'processes', and noted that as well as being variable in form around the gill basket in the mullet (*Mugil cephalus*), they change with age in the mackerel (*Scomber japonicus*) and the sardine (*Sardinops melanosticta*) as their diets alter. De Ciochomski made similar observations in comparing the gill raker ontogeny of two species of *Engraulis* (1967). Van den Berg *et al.* (1994c) also noted preservational problems of 'needle teeth' in contemporary fish populations, in terms of incomplete ossification of needles, which would clearly hinder assessment of their presence or absence within the fossil record. Suspension feeding can develop independently several times within a given clade of fish (Nelson 1967) appearing to be a common strategic response to the availability of food suitable for microphagy (Lazzarro 1987). Similarly, the development of 'needle teeth' on gill rakers in edentulous fish appears to have occurred independently among different clades of suspension-feeding fish, and as such its use as a taxonomic tool can only be a limited one.

The origins of the use of 'needle teeth' as a diagnostic character for pachycormids relates to the occasional use of basking sharks as modern analogues for *Leedsichthys*. In

comparatively early studies on basking sharks, van Deinse & Adriani (1953) noted the retrieval of some specimens of *Cetorhinus maximus* during the winter months without any gill rakers, and even tentatively suggested that a new form of basking shark might have been found, for which they provisionally proposed the name *Cetorhinus maximus infanuncula* nova forma. To counter this, Parker & Boeseman (1954) hypothesised that *Cetorhinus maximus* simply shed its gill rakers (fig. 6.5) during the winter, a hypothesis that has since been rejected (Sims 1999). It was this hypothesis that was the model for Martill's (1988) suggestion that periodic shedding of 'needle teeth' occurred from the gill rakers of *Leedsichthys*. This model was proposed, because of a variability in gill rakers of *Leedsichthys problematicus* recovered from the Oxford Clay, as not all of them had 'needle teeth'. In fact, when the hypodigm of material attributed to *Leedsichthys* is reviewed, only one specimen (that figured by Martill (1988), PETMG F34, consisting of a partial skull with damaged remains of skull roof, branchial basket and jaws) has ever been recovered with needle teeth present, despite the almost ubiquitous occurrence of gill rakers with specimens of this taxon. As such, it was decided to reexamine this specimen, to assess other aspects of its gill raker and general anatomy.

Lambers' 1992 analysis of the interrelationships of Pachycormiformes used the presence or absence of 'needle teeth' on the gill rakers as a character. For his analysis he scored two taxa as possessing 'needle teeth' – one, following Martill (1988) was *Leedsichthys*, the other was *Asthenocormus*. This latter genus is known from only a handful of 1-2 metre long individuals from the Tithonian Solnhofen limestone, and only one of those specimens, in the Leich collection (L.1309), features putative gill rakers. This occurrence is reviewed and assessed below.

With the demonstrated weaknesses of gill raker morphology as a source of taxonomic characters, it is perhaps worth examining the validity of the second species of *Leedsichthys*, which was based solely on variations within gill raker structure from the 'norm' for *Leedsichthys problematicus*. Martill *et al.* (1999) based the new taxon of *Leedsichthys notocetes* from the Oxfordian of Chile on the characteristic fenestrae that occurred within the ramus of the gill rakers, that were absent from the gill rakers known from the Oxford Clay specimens of *Leedsichthys*. The presence of such fenestrae is counter-intuitive – why would a structure subjected to comparatively high hydrodynamic pressures during suspension-feeding have such a structural weakness as holes, just at the level of the functional ridges, making it likely that they would fail and detach? The gill raker would be expected to be subject to intense hydrodynamic distortion (MacNeill &

Brandt 1990; Wright *et al.* 1983) in high flow velocities and therefore be subject to strong selection against anything that would structurally weaken the convex leading surface. Conversely, the presence of these fenestrae could be the manifestation of a natural shedding process, as proposed by Martill (1988). Recent work has demonstrated through the examination of marks of skeletal growth (see Chapter 7) that gill rakers did not shed seasonally in *Leedsichthys*, but were retained for much (if not all) of the life of the animal. The appearance of such fenestrae might, however, be a sign of incipient shedding of the functional dorsal section (including the ridges) of the rakers of this animal, as new growth produced more bone to replace this structure. To assess this, the holotype block of gill rakers for *Leedsichthys notocetes* (SMNK 2573.PAL) was reviewed, and compared with the gill rakers that form part of the holotype specimen of *Leedsichthys problematicus* (BMNH P.6921).

6.3 - GILL RAKER MORPHOLOGY OF *LEEDSICHTHYS* AND SELECTED PACHYCORMID SPECIMENS

This section details the morphology of four key specimens, with particular reference to their implications for the use of gill raker morphology in taxonomy.

6.3.1 - A) Comments On Holotype (BMNH P.6921) Gill Rakers

In order to assess how significant the morphological differences may be between *Leedsichthys problematicus* and specimens PETMG F34 and SMNK 2573.PAL, it is necessary to examine the series of 89 gill raker elements that constitute part of the holotype specimen of *Leedsichthys problematicus*, BMNH P.6921. Of this series, only two elements are complete (with base, stalk and tip intact), representing different extremes of size: the short gill raker is 39mm long, the long gill raker is 112mm long. More than a century after this specimen was first described, only one intact gill raker within the known hypodigm has been found that is shorter (a 35mm raker in BMNH P.10000), and only two that are longer (see Chapter 7 and Appendix VII) (fig. 6.2). In 1890, Smith Woodward (1890b) figured two of the fragments, and repeated the account of them from his original description (1889b), describing them as "laterally compressed, slightly expanded at the basal extremity, and rarely straight, but irregularly bent or contorted. The surface is coarsely rugose, and one long border is rounded, while the other is cleft by a longitudinal median furrow. The rounded border is comparatively smooth, but the furrowed edge is coarsely serrated, a series of short oblique ridges terminating in points on each side." Smith Woodward's figure showed the features he described (1890b), with his diagram 10a

showing a plan view of the longitudinal median furrow – the 'dental groove' of Martill (1988). This furrow (fig. 6.3) is shaped by the lateral and medial borders, which are composed of a series of fimbriations forming a pair of external ridges (fig. 6.2), occasionally with intergrowth between fimbriae (fig. 6.1). This creates the effect of an undulating ridged flange (fig. 6.7C) on each side of the dorsal surface of the gill raker. The fimbriae may radiate at the tip to point directly into the interarch gap (fig. 6.2), growing in a long tongue-like fashion. In terms of Yasuda's scheme (following Yasuda's table of 'processes', 1960) these features curve up as biserial lateral growths resembling the 'processes' depicted for adult *Scomber japonicus* (1960: Fig. 4A) flanking a groove.

There is, however, more than one gill raker morph present within the 89 gill raker fragments of the holotype. There are gill rakers (including the longest gill raker element present) that lack the groove described by Smith Woodward (fig. 6.4), as though it has been occluded through the two lateral edges growing together. In some cases, this feature appears to become even more removed from the furrowed state (fig. 6.3), with the oblique ridges seeming to become a plane perpendicular to the axis of the stalk, with the lateral and medial edges of the ridges becoming less thick and oblique and more thin and vertical, resembling a sharp elevated blade that runs transversely from one side of the raker to the other, as though fimbriae on opposite borders have grown together. This character has also been noted on isolated gill rakers from the Callovian of Normandie (fig. 6.9A,B) and the Kimmeridgian of Le Havre (G.1073J, fig. 6.10), which have been referred to *Leedsichthys*. Within Peterborough Oxford Clay material, this character can also be seen in occasional raker fragments within specimens LEIUG 96087/24 and BMNH P.8610. Within the last two specimens and BMNH P.6921, a continuum of forms exists between the two extremes.

In addition, it is worth noting that the isolated gill raker element from the Callovian of Normandie also appears to preserve traces in plan view of an extremely thin mesh above the gill raker, as though growing out from the tips of the transverse planes (fig. 6.9C). It is probably simplest to regard this as a delicate component that is not preserved in the softer Oxford Clay around Peterborough, rather than a morphology unique to the Callovian of Normandie.

6.3.2 - B) Description Of PETMG F34

PETMG F34 is an enigmatic specimen, previously referred to *Leedsichthys* (Martill 1988), but it does not appear to have any definitive dermatocranial morphology to diagnose that it is *Leedsichthys*: it is only partially freed from its clay matrix, and lacks distinctive

perimeters to the bones of its skull roof. The specimen is a 475mm by 175mm block of two parts (fig. 6.13A,B), representing the bulk of the gill basket of a single individual with associated dermatocranial elements. Identifiable cranial elements on the dorsal aspect (fig. 6.13A) include a 153mm by 77mm complete left parietal, and parts of a left maxillary fragmented through transverse shear. The jaw elements suffer from having the occlusal (potentially tooth-bearing) surfaces hidden or sheared away, so that it cannot be confirmed that these elements were edentulous. Although the parietal conforms to a recognisable shape, the maxilla cannot easily be related to the only known *Leedsichthys* maxilla (GLAHM V3363) or any other known jaw element. Assuming that these fragments are correctly identified, then the lower jaw is lost from this specimen.

No specimen of *Leedsichthys* presents a similar form of gill raker (or even gill basket) structure to that presented by PETMG F34. The anterior parts of the gill basket (the hypobranchials, hypohyals and the anterior tips of the ceratobranchials) are missing, but the posterior extremities of right ceratobranchials I and II are characteristically present on the inferior surface of the posterior block (fig. 6.13B) with associated, exceptionally long, gill rakers, as in the large adult gill basket of *Leedsichthys* (BMNH P.10156 – Liston 2005). The ceratobranchials strongly resemble those in the subadult specimen BMNH P.11823 (see Chapter 7) in form, although they are significantly smaller (a maximum width of 40mm, compared with the maximum ceratobranchial width of 49mm in the subadult specimen). The gill rakers between the ceratobranchials show an average spacing (King & Macleod 1976) of 5.3-7.3mm, which is not dissimilar to the figure for the gill basket specimen BMNH P.10156 (6.6-8.2mm) and the Antofagasta articulated partial gill basket (fig. 6.12, 5.8-6.2mm). The gill rakers have a very similar orientation (angle subtended by the gill raker to the axis of the ceratobranchial is around 45 degrees) to those in the gill basket specimen BMNH P.10156, but are considerably shorter, with an average length of around 45mm instead of 75mm. The extended gill rakers also differ significantly in their lengths, with a maximum length (at the posterior termination of ceratobranchials I and II) in PETMG F34 of 75mm, and 135mm in BMNH P.10156. The gill rakers also differ in form, with a strong right-angled bifid base connecting them to the ceratobranchial, instead of the gently curved transition from a leaf-shaped base seen in all other gill rakers of *Leedsichthys* that retain their bases. In addition, each gill raker preserves a series of 'needle teeth' on the dorsal surface of the stalk (fig. 6.14). Some rakers exhibit signs of a slightly raised edge medial and lateral to the line of 'needle teeth', which may be the developmental start of a shallow median groove (fig. 6.15, centre of image). Frequently, if a 'needle' has become detached from its gill raker, a socket-like recess is revealed (fig.

6.15, centre left and centre right of image). Although following Yasuda's scheme (1960) the 'needle' is very similar to the long and pointed morph of *Seriola quinqueradiata* depicted by Yasuda (1960: Fig. 4D), it appears that, being centrally rather than laterally or medially located on the dorsal surface, the 'needle teeth' are not homologous structures to the dorsal surface structures described as 'processes' (Yasuda 1960), 'barbs' (Peck 1893), or 'teeth' (Gibson 1988) in other fish. To distinguish them from these other structures, the term *acus fanunculorum* (needle of the raker) will be used to describe the pointed central structure set within a groove, in some areas appearing almost 'gripped' by the slightly serrated or peg-like edge of the lateral outgrowths on the gill raker (which are the true homologue of the features of Peck, Yasuda and Gibson), the pegs alternating with each *acus* (fig. 6.15, centre of image).

The small but significant departures from the gill raker morphology observed in other specimens of *Leedsichthys problematicus* can all be explained for this specimen on the grounds of size and ontogeny, except for the presence of the *acus fanunculorum* and the unusual transition from base to stalk. These characters could be present in this specimen for three possible reasons: the specimen could be unusually well-preserved; the characters could result from taxonomic differences; the characters could be part of an ontogenetic sequence leading to the more conventional morphology of *Leedsichthys problematicus* gill rakers.

The condition of the matrix does not lead one to believe that this is a case of exceptional preservation, as the specimen is very much like any Peterborough Member Oxford Clay vertebrate. It is unusual that it has been possible to excavate the branchial elements as a collective unit, and it is unique to excavate them with dermatocranial elements articulated. It could be that the unusual retention of the parietal with the carcass has led to it limiting the post mortem disruption of the branchial basket. This alone would be unlikely to explain the degree to which the hundreds of gill rakers have been retained in position with *acus fanunculorum* intact, compared to other specimens of *Leedsichthys problematicus*. Of these other specimens, only BMNH P.10156 retains some gill rakers in position, and it is preserved in a concretion. All other specimens have ceratobranchials that are devoid of gill rakers. One could speculate that with increasing size, the greater thickness of the connective tissue and epithelia covering the ceratobranchials meant that the gill rakers detached more easily from them after death, but there is not enough evidence to support this contention. Similarly, the base/ceratobranchial transition is not well enough exposed

in specimens of *Leedsichthys* (i.e. BMNH P.10156) to be certain that the right-angled base does not occur at some point in the gill basket.

In summary, although PETMG F34 may represent a new taxon, it is equally possible that the *acus fanunculorum* represents an early ontogenetic stage in the development of *Leedsichthys problematicus*.

6.3.3 - C) Comments On The Leich *Asthenocormus*

The Leich Collection specimen (L.1309) of *Asthenocormus* contains clusters of disarticulated fragments in the proximity of the head of a complete individual (Lambers 1992), some bearing tooth-like points that have been identified as possible gill rakers with 'needle teeth' (fig. 6.16) (Lambers 1992) of a form similar to a swollen-based version of the morph for *Seriola quinqueradiata* depicted by Yasuda (1960). If they are gill rakers, then they are extremely fragmentary. It is possible that they represent ectopterygoid dentition or pharyngeal tooth plates, or may not even belong to the individual that occupies the bulk of the slab. Be that as it may, no *in situ* gill rakers (with or without 'needle teeth') have ever been recorded for *Asthenocormus*, despite the specimens coming from the exceptionally well-preserved material in the Tithonian Solnhofen Lithographic Limestone.

The presence or absence of 'needle teeth' on gill rakers in pachycormids is a character which should be easiest to assess in the larger taxa of *Asthenocormus* and *Leedsichthys*, when the size of the fishes makes gill rakers easy to detect and examine, and yet the evidence is equivocal as to whether or not either of these taxa possessed such 'needles'. There is also no specific reference made (Lambers 1992) to the 'needle-less' gill raker state in the other smaller pachycormids. As such, the presence/absence of these 'needle teeth' is a character that cannot be rigorously or consistently demonstrated for either larger or smaller (e.g. *Sauropsis*, *Haasichthys*) representatives of the family.

Given how problematic the characters of gill rakers have proven to be in contemporary fish (above), how variable the character of needle presence/absence appears to be in the few cited examples of contemporary fish, and the limited possibility of assessing the presence of the character in most members of the Family Pachycormidae, it is suggested that this character should not be included in a revised analysis using Lambers' dataset, as it may be distorting the hypothesis presented by Lambers (1992).

6.3.4 - D) Description Of SMNK 2573.PAL

The six surfaces of SMNK 2573.PAL from the Atacama Desert in Chile are extremely irregular, and around 38 gill raker fragments are visible on the upper surface (fig. 6.17). From an initial examination, it is clear that none of the gill rakers on the block are complete: in the sense of the plan of a generic gill raker (fig. 6.6), none of the fragments have all of the basic components present, hence it was necessary for Martill *et al.* to composite a reconstruction from several of the fragments on the block (1999, Fig.4). The fimbriated character of the lateral and medial surfaces is again evident, displaying the same long curling tongue-like growth at the the tips (fig. 6.18B,D). In terms of Yasuda's scheme (following Yasuda's table of 'processes', 1960) these features curve up as biserial lateral growths resembling the 'processes' depicted for adult *Scomber japonicus* (1960: Fig. 4A) flanking a groove, as with the gill rakers of *Leedsichthys problematicus*.

Martill *et al.* (1999) described the 'sub-oval fenestrae' as a character of the lateral surface of the gill rakers, with a fenestra situated at the base of each plication along the length of the stalk (*sensu* Kazanski and Peirong) of the gill raker. The gill raker fragments on the block do not universally share the fenestral character, indeed, the fenestrae are only clearly evident on areas of four of the fragments (fig. 6.18A-D). Even the most extensive of these fragments (fig. 6.18A) does not present the fenestrae as described by Martill *et al.* in their composite diagram. In reality, the fenestrae are only visible in sections of the gill rakers, and when they are present, they appear to grade smoothly back into a regular raker only a few oblique ridges further along the stalk. Within the height of an average ridge-bearing stretch of the gill raker stalk, the oblique ridges occupy around 3mm out of the 9mm height of the element (fig. 6.18A) with a 2mm height below this level, where the fenestrae might manifest, and a more solid 4mm extent of stalk below that (fig. 6.18A). Although the fenestrae shown in the diagram of Martill *et al.* would ideally be formed by the oblique ridges anterior and posterior to them, in reality these walls commonly are incomplete, with the rim of the fenestra of variable thickness, and anterior or posterior walls often partially or completely absent (fig. 6.18A-D).

On close examination it can be seen that the sections where the fenestrae appear to present are actually at a different topographic level to the rest of the remains on a given gill raker (fig. 6.18A). This is because the gill raker is an area of weakness within the calcilutite block, and the block has preferentially split through, rather than around, the periosteal surface of the gill rakers. This means that the outer surface is rarely preserved intact, as has also been observed with other material from a different region of the Atacama Desert

in Chile (Arratia & Schultze 1999; Liston 2004a; see Chapter 4), where the harder matrix surrounding the more fragile gill rakers and other fossilised bones generally fractures through the fossil material, rendering excavation and reconstruction of the fossil material extremely problematic (see Chapter 4). Thus there is longitudinal damage to each and every fragment – in no gill raker fragment is the external surface visible or intact, and the bone always shows signs of breakage. The 'sub-oval fenestrae' are an artefact on the specimen (Steel, pers. comm. 08/2004), formed by fracturing and/or erosion penetrating the thin gill raker walls between the oblique ridges to partially expose the internal gill raker cavity (figs. 6.19B,6.21). The internal gill raker cavity is formed by extensive bone resorption (see Chapter 7), and is irregularly exposed across the gill raker, depending upon the gill raker's topographic exposure and vulnerability to erosional or mechanical damage to the block. This model is further supported by other similar gill raker material from the Oxfordian of Chile (fig. 6.11,6.12) (Arratia & Schultze 1999; Liston 2004a; see Chapter 4), which preserves the same characteristics as displayed on the SMNK 2573.PAL block, including intermittent and occasional 'fenestrae' on its ventral as well as lateral and medial surfaces (fig. 6.19A). This occurs on the ventral surface in this specimen, because the rakers are not isolated, but are lying stacked *en echelon* more or less vertically, as they would have been in life. This means that there is more erosional attack from above (on to the ventral as well as the lateral surfaces), as the gill rakers formed a fracture plane through the rock.

If the fenestral level of the gill raker is regarded as a 'box' formed of an upper surface (the bone forming the base of the 'dental groove' of Martill *et al.* fig.4c), a lower surface (the bone covering over the 'microspongiosa' of Martill *et al.* fig.4c), a left surface (lateral or medial wall of raker), a right surface (the opposite wall of the raker), and anterior and posterior partial planes of bone (the four oblique ridges forming the four verticals of the box), then each gill raker has had either the left or right wall excised through fracturing or erosion. As noted by Martill *et al.* (1999), the stalk of the raker is "thin-walled and hollow dorsally, comprising two parallel sheets of bone." It is the centres of these thin lateral walls of each subacular chamber that have broken away under shear, revealing the matrix-filled hollow dorsal chamber described. The reason why anterior and posterior bony rims partially appear as apparent struts, is because they represent the internal thickening of the oblique ridges of Smith Woodward (1889b, 1890b) or plications of Martill *et al.* (1999).

The level at which the fracturing has occurred has determined how thick the 'walls' of the fenestrae (the 'frames' around the 'windows') have appeared. This also explains why that

(circa 2mm) level of the gill raker lateral or medial surface grades from bony external wall, to parallel oblique ridges, to fenestrae, to sediment that extends uninterrupted through the internal gill raker cavity at the level of the ridges: the fracture sheared through the raker at an angle close to (but not quite) the axis of the gill raker, removing an entire side of ridges and penetrating further into the middle of the gill raker as it progressed. An analogy might be helpful – if one sectioned through the hull of a ship longitudinally, one is far more likely to cut through the bulkheads that partially separate different sections of the ship's hull, rather than through the thickness of the port or starboard hull. The 'bulkheads' in the gill raker are the internal thickening to support the oblique ridge on the external surface of the gill raker, which is why the angle of the ridges reflects the orientation of the fenestrae. The patchy exposure of fenestrae on each raker that exhibits them, reflects the degree of internal resorption within the bone of the gill raker, as well as the fracturing and differential delamination of the gill raker eroding in a harsh desert weathering regime (as opposed to a frequently water-logged Oxford Clay, which is more likely to separate around rather than through a fragile structure such as a gill raker), thus creating the illusion of regularly-spaced fenestrae.

This is further supported by another area of evidence: on this block, if bone has been in direct contact with the calcilutite, and has then broken away, it leaves behind a black contact mark (fig. 6.20). On the most prominent example of a gill raker with fenestrae on the upper surface of the block, the lateral aspect is against the matrix, with medial aspect uppermost (fig. 6.18A). Taking into account the relief in the raker, it is evident that it is the inner surface of the lateral wall of the gill raker that is visible proximally (fig. 6.18A, area A) for the most part, displaying the ridges separated only by slits of matrix. It is only at an area of high relief (fig. 6.18A, starting at area B), where the fracture is passing through a more medial part of the raker, that the fenestrae become visible. The above trend can be seen from fenestrae on a high relief section with black areas showing (fig. 6.18A, area C) where more complete areas of bone once completely and partially (depending on which chamber is being referred to) enclosed the chambers (fig. 6.18A, area D), to parallel ridges on the most distal (fig. 6.18A, area E) extent of the raker stalk.

It appears that it is the differences in matrix and exposure regime that have led to this material presenting differently to that from known Callovian-Kimmeridgian age sediments. Another difference is that the material from Chile can also present a finely-preserved ultrastructure intimately associated with the gill rakers (variably visible on some areas on the block fig. 6.17, fig. 6.22, as well as a separate fragment and thin sections showing it in

transverse fig. 6.23, fig. 6.25B and plan views fig. 6.24, fig. 6.25A). This unusual ultrastructure bears some resemblance to the suspension-feeding meshes of the contemporary fishes *Rhincodon typus* the whale shark (Gudger 1941 fig. 8) and the advanced suspension-feeding silver carp *Hypophthalmichthys molitrix* (Verigin 1957 fig. 1), and may be associated with increased efficiency of suspension feeding (Wilamovski 1972), through extraction of finer organic material. This latter species (Oshima 1919) is one of many suspension-feeders that have independently evolved epibranchial organs (Sanderson & Wassersug 1993), and has a remarkable internal '3-way extraction system' (Peirong 1989, Gerking 1994), enabling it to feed on phytoplankton as well as suspended bacteria (Sanderson & Wassersug 1993). This mesh feature or characteristic has partially been observed in only one *Leedsichthys* specimen from the Callovian-Kimmeridgian age clay deposits, perhaps due to preservational factors. This specimen, from the Callovian of Normandie, can show an identical plan view (fig. 6.9c) to the mesh above the gill rakers in Oxfordian material from Chile (fig. 6.24). Another specimen (BMNH P.10000) has a gill raker that appears to have the lower part of a mesh originating from inside the median furrow (fig. 6.26) but the white colour of the structure, despite its apparent contiguity with the lateral edges of the gill raker, may mean that it is a curiously juxtaposed elongate piece of invertebrate shell, rather than part of the gill raker itself. Further work to analyse the nature of the structure in this raker via SEM, and indeed to reconstruct the apparent 'supra-fanuncular mesh' atop the gill rakers in *Leedsichthys*, may well give indirect evidence of the predominant prey-size in the environment, a rare indication in our sparse knowledge of the geological record of planktonic lifeforms (Cressey & Patterson 1973).

6.3.5 – Validity of Gill Raker Morphology as a Taxonomic Tool

Gill rakers have been demonstrated to be a poor source of taxonomically valid characters: they change their form with age and in response to environmental stimuli. They are also a high-risk character to base new taxa on due to the likelihood of convergence. From a preservational sense, gill rakers can be subject to damage (resulting in artefacts), or be obscured by other remains. The 'needle teeth' of gill rakers may not fully ossify in life (van den Berg *et al.* 1994c), and within *Leedsichthys* it is unclear whether their presence in specimen PETMG F34 is the result of exceptional preservation of an average specimen, the rare preservation of a subadult form, or the characteristic of a hitherto undescribed taxon. Given that fish go through many structural changes in their gill rakers throughout ontogeny, that Webb & de Buffrenil (1990) have noted that "...the larger the adult size, the larger the number of intermediate stages that might be expected" in the development of an animal, and in the absence of evidence that a *Leedsichthys problematicus* bearing a gill

basket as small as indicated by PETMG F34 would have a different form of gill raker present, it seems most practical to refer to this specimen as a subadult of this species, rather than argue for it to be another new osteichthyan taxon with hypertrophy of the gill rakers in the Oxford Clay sea (Liston 2005). Whether it is a new taxon or the youngest form of *Leedsichthys problematicus* that has yet been seen, it is clear that the presence or absence of 'needle teeth' in gill rakers does not indicate the presence or absence of *Leedsichthys problematicus* in an environment. Similarly, the evidence for *Asthenocormus* (and the genus represented by BMNH P.61563, referred to here as 'Taxon 13', Liston 2005) bearing 'needle teeth' on its gill rakers is not entirely convincing.

Conversely, the gill raker material on the block SMNK 2573.PAL described as *Leedsichthys notocetes* seems virtually identical to specimens referred to *Leedsichthys problematicus*, with three caveats:

i) The suprafanuncular mesh (fig. 6.22). There is some evidence for the presence of this in Callovian *Leedsichthys problematicus* gill rakers, but it is hard to tell if the material is more developed in the Oxfordian material from the Atacama desert, or simply more suited to preservation in that lithology. Alternatively, it may again be an ontogenetic development, as with increasing age the animal develops a finer mesh to make its extraction of organic material from the water more efficient, and so support an increasing adult body mass. This pattern of development is seen in the Silver Carp *Hypophthalmichthys molitrix* (Wilamovski 1972).

ii) The presence of fenestrae, which appear to be an erosional artefact (fig. 6.18A).

iii) The degree of internal bone resorption and remodelling within the gill rakers (fig. 6.21). This internal resorption seems more extensive than in other gill rakers recently examined for analysis of growth rings (see Chapter 7), but this may well be more of a reflection on the different positions chosen to section the gill rakers for analysis, than on fundamental differences between the gill rakers themselves.

This material (SMNK 2573.PAL) is therefore probably referrable to *Leedsichthys problematicus*. More extensive material with similar gill rakers has been collected from elsewhere in the Oxfordian of Chile (Arratia & Schultze 1999, Liston 2004a, see Chapter 4) and is currently awaiting preparation. This should give a clearer indication of whether or not there are any significant taxonomic differences between the European and the South American *Leedsichthys* material. To create a separate taxon on the basis of the evidence currently available would be to unnecessarily increase taxonomic names on the basis of very little evidence (Strand 1928, Fowler 1930).

6.4 – PHYLOGENY OF THE FAMILY PACHYCORMIDAE

In the light of the problems presented above with using characters of gill rakers for taxonomic purposes, Lambers' dataset was revisited to determine whether the presence of this character might be the source of an inappropriate linkage between *Leedsichthys* and *Asthenocormus*. Given the lack of common bone morphologies between *Asthenocormus* and *Leedsichthys*, and the apparent presence of such morphologies in *Saurostomus* and *Leedsichthys*, it seemed that this dubious gill raker character might be responsible for indicating a spurious relationship between *Leedsichthys* and *Asthenocormus*.

Following on from the work of Lambers (1992), *Caturus* has been specified as the outgroup in all tree-building exercises. This taxon has long been closely-linked with the pachycormids, Gardiner (1967) stated that all Amiiformes and the "aberrant Pachycormiformes" came from the Caturidae, and as recently as 1988 Bartsch stated (in direct opposition to Patterson 1973) the not generally accepted view that pachycormids were in fact caturids. Including this outgroup taxon, a total of thirteen taxa (ranges of taxa are given in Appendix II) were used, including a new taxon (description in Press – referred to here as 'Taxon 13'): *Sauropsis*, *Euthynotus*, *'Hypsocormus macrodon'*, *Orthocormus*, *Protosphyraena*, *Asthenocormus*, *Leedsichthys*, *Hypsocormus insignis*, *Pseudoasthenocormus*, *Pachycormus*, *Saurostomus*, 'Taxon 13'. This is not exhaustive of all currently-described pachycormid taxa for which extensive skeletal material is known – data are not yet available for the recently-described Toarcian form *Haasichthys* (Delsate 1999) or the as yet undescribed Turonian pachycormid from Mexico (Blanco-Piñón *et al.* 2002, 2003, 2005).

Lambers (1992) reviewed Mainwaring's (1978) dataset, discarding some of her characters and adding others. He used fifteen characters to examine the interrelationships within the pachycormids, and a further sixteen to define the pachycormids as a discrete group. All characters are listed in aAppendix III (and see also Appendix I).

Characters examining interrelationships between pachycormids:
Characters 1 and 8 were skull roof characters.

Characters 2-6 were dentition-related.

Character 7 was based on the presence/absence of gill raker teeth.

Characters 9, 10, 12 and 13 were fin-related.

Characters 11 and 16 were related to fin plates.Characters 14 and 15 were meristic characteristics of the axial skeleton.

The dataset was not entirely complete – the taxon *Leedsichthys* only had two characters completed (7 and 13), the rest being scored as unknown ('?'). Eight of these unknown character states have been recoded for this taxon for use in this study.

Revision of characters – characters 3 and 4 dealt with characteristics of premaxillary dentition that did not appear to be independent, based on the results in the matrix. As such, they were combined into one character for this analysis.

The utility of character 7 relies on being able to detect the presence of gill raker 'needle teeth', which as already noted has preservational (variable ossification potential) as well as practical (size and relative exposure of feature) problems associated with it. Even between different specimens of *Leedsichthys*, for example, whether these features are preserved or not varies considerably, indeed only very occasionally in any pachycormid have the features necessary for such a determination been preserved. As is noted for contemporary fish (van den Berg *et al.* 1994c) there is great variation in the ossification, and therefore the potential for preservation, of these features. As such, character 7 was dropped from the matrix, to examine whether it was causing an unfair linkage between *Leedsichthys* and *Asthenocormus*.

6.4.1 - Characters describing pachycormids as a discrete group:

In scoring character states for *Leedsichthys*, it was noted that two of the character states did not conform to the symplesiomorphic pachycormid 'condition' defined by Lambers. This calls into question the use of squamation and the presence of the hypural plate as defining characters for the group. Pending further investigation, they were removed from the matrix of characters to be used.

6.4.2 - New Characters:

Across the pachycormids, there is observable variation in the degree of ossification of different parts of the skeleton. This pattern is made particularly evident by another tendency within the group, towards relatively large (>1 metre Standard Length) adult size.

The trend towards unsegmented fin-rays is juvenile in character (Haas 1962) in a similar way to the reduction in ossification, and may be part of a paedomorphic trait within the group. In order to further examine the interrelationships of the group, the numbers of lepidotrichia occurring at the base of the caudal, dorsal and pectoral fins were recorded for each taxon (e.g. Greenwood 1962, Bannikov 2006). As the remaining group-defining characters were parsimony uninformative for the purpose of analysis of interrelationships within the group, they were not used.

Data were compiled on a PC using Nexus Data Editor (NDE) version 0.5.0 (Page 2001a) and analysed using PAUP 4.0b12 (Swofford 2002), with characters ordered and unweighted. Due to the small size of the dataset, branch 'n' bound was used. Within each taxon, characters that could not be scored due to lack of information were recorded as '?' and treated as missing data in the analysis. Characters scored for more than one state in a taxon were treated as polymorphic. Trees were analysed using TreeView version 1.6.6 (Page 2001b).

6.4.3 - Cladistic Analysis

The total matrix produced (35 characters for 13 taxa – a full listing of all 35 characters is included in the Appendix) comprised 455 cells of which 8.8% contained ambiguous data. The condensing of both premaxillary dentition characters into a single character, and the exclusion of the questionable 'needle teeth' character along with Lambers' group-defining and other parsimony uninformative characters, left a reduced 16 character set, with 8.7% ambiguous cells.

Not all taxa currently recognised as members of Family Pachycormidae were included, as some are fragmentary (e.g. *Neopachycormus* of Taverne 1977), and others have not yet had their character states scored according to Lambers (e.g. *Haasichthys* of Delsate 1999). Of the taxa used, the least complete was *Protosphyraena* on 37.5% unscored, followed by *Leedsichthys* on 31.25%. Only 4 of the characters in the dataset (new C2, 5, 6, 14) were unambiguously coded for all 13 taxa. Ambiguous cell frequencies reached a maximum of 46-50% in C16.

In initial analyses, the character of gill raker 'needle teeth' presented as ambiguous between ACCTRAN and DELTRAN, further supporting its exclusion from the final test of the refined dataset.

For comparison, the strict consensus tree for the 46 most-parsimonious trees (34 steps in length – fig. 6.27) and 50% majority rule (fig. 6.28) from Lambers' original (fifteen character) dataset is shown. Lambers' original dataset of characters discriminating between pachycormids for the original 12 taxa produced 5 most-parsimonious trees of 29 steps in length. Addition of the thirteenth taxon increased the step length to 38, but retained 5 most-parsimonious trees. Addition of character 35 (rib ossification) similarly did not affect the number of most-parsimonious trees, but addition of the three fin-ray characters caused the number of most-parsimonious trees to increase to 76 (of 47 steps). With analysis of all 35 characters for all 13 taxa the number of most-parsimonious trees dropped to 15, of 66 steps in length. The reduced (16) character dataset produced 45 most-parsimonious trees (41 steps in length, C.I. 0.585, R.I. 0.638), with the following strict consensus tree (fig. 6.29) and 50% majority rule tree (fig. 6.30). This strict consensus was accepted as my phylogenetic hypothesis.

6.5 - DISCUSSION

The phylogenetic hypothesis presented in the strict consensus tree (fig. 6.29) endorses and strengthens Lambers' (1992) in the following areas: more support is shown for the grouping of the edentulous pachycormiformes {*Asthenocormus*, *Leedsichthys* and Taxon 13} with *Pachycormus* and *Saurostomus* (presence in most-parsimonious trees increased from 72%-96%); similarly, the cluster of '*Hypsocormus macrodon*', *Orthocormus* and *Protosphyraena* is consolidated (presence in most-parsimonious trees increased from 76%-100%) with the further inclusion of *Hypsocormus insignis* (100%).

Pseudoasthenocormus's relationship to this cluster remains unclear, with *Sauropsis* and *Euthynotus* remaining distant from all other groupings. Running an analysis of leaf stability using RADCON (Thorley & Page 2004) on 8,000 unrooted trees identified these last three genera (as well as *Protosphyraena*) as the most unstable taxa within the dataset.

However, when subjected to decay analysis, the data is not robust, with an increase of one step causing an unresolved bush. Under Double Decay Analysis (Wilkinson *et al.* 2000), {*Asthenocormus*, *Leedsichthys* and Taxon 13}, {*Pachycormus* and *Saurostomus*} and {'*Hypsocormus macrodon*', *Orthocormus* and *Protosphyraena*} all have 2-step support. {*Asthenocormus* and Taxon 13} has 3-step support, and this is the most robust clade in the tree.

In terms of the dubious role of Lambers' character 7 (presence/absence of gill raker 'needle teeth'), removal of this character did not harm the linkage between *Asthenocormus* and *Leedsichthys*, indeed the introduction of 'Taxon 13' linked all three taxa together in 100% of the most-parsimonious trees. This branch of the tree presumably reflects an increasing functional burden and canalization through edentulousness, narrowing evolutionary prospects of the group (Riedl 1979).

Two clear monophyletic groups emerge within this tree (fig. 6.29), consisting of the edentulous Pachycormiformes (Node A in fig. 6.29 or 'g' in fig. 6.31 – defined by absence of dentition and caudal fin segmentation) and the tusked Pachycormiformes (Node B in fig. 6.29 or 'c' in fig. 6.31 – defined by tusk-like rostrodermethmoid dentition with falcate and extended anal fin). Unexpectedly, a third group, *Pachycormus* and *Saurostomus*, which would be expected to be clustered close to the edentulous Pachycormiformes due to their similar osteology (Liston 2004a, Smith Woodward 1916), does not appear in that position in the strict consensus tree, in spite of it being a common (96% support for this linkage in the majority rule consensus) but not universal hypothesis. The presence of a temporal boss, absence of pelvic fin, and the presence of a double row of supraneurals are three character states that *Leedsichthys* shares with these two genera.

Omitting *Sauropsis*, *Euthynotus* and *Pseudoasthenocormus* and repeating the analysis using all thirteen taxa and the 16 character dataset reduced the number of most-parsimonious trees from 45 of 41 steps in length to 5 most-parsimonious trees of 31 steps in length, with nodes A and B present in all five trees, and only the relations of (*Pachycormus* + *Saurostomus*) within the tree varying.

An evolutionary tree was constructed (Smith 1994) in order to demonstrate the stratigraphical distribution of the taxa and their hypothesised relationships (fig. 6.31). The more problematic of the tusked Pachycormiformes were omitted from this tree for clarity. As noted earlier, the dataset does not include all described pachycormid taxa, and it is hoped that more material can be retrieved for some of the partial Cretaceous pachycormids that have been recovered (Taverne 1977, Lambers & Boekschoten 1995, Blanco-Piñón *et al.* 2002, Yabumoto 2005) to increase our understanding of this group's diversity throughout this period.

Genus *Pachycormus*, despite a thorough analysis of its skull variation by Mainwaring (1978), still has some surprising variation within its post-cranial skeleton (pers. Obs.),

suggesting that perhaps the taxonomy of this genus requires further work. Similarly, resolution of the problematic taxon *'Hypsocormus' macrodon* (see Lambers 1992 for a full discussion) would be helpful for future workers.

6.6 - CONCLUSIONS AND FURTHER WORK

The referral of PETMG F34 to *Leedsichthys problematicus* remains uncertain, given that no skeletal elements of *Leedsichthys problematicus* are identifiable within the specimen beyond the gill rakers and these possess anomalous *acus fanunculorum* which are not known in any other recognised specimen of *Leedsichthys*. This does not, however, exclude the *acus fanunculorum* from being present in an early ontogenetic stage in the development of the gill rakers in this taxon. Regardless of this, it seems that gill rakers should not be used as a primary basis for diagnosis of taxa. Gill rakers are complex and diverse structures, and it is difficult to use aspects of them as characters without having a clear understanding of their variations throughout a given taxon's gill skeleton, as well as variations throughout the ontogeny of an individual taxon. To fully determine the occurrence or otherwise of 'needle teeth' (whether *acus fanunculorum* or other forms) in pachycormids, as in other groups, a full knowledge of the appearance in each taxon is necessary to determine how ephemeral the character may be. Fortunately, there are some prospects for progress in this area, at least with regards to *Leedsichthys*. A specimen collected recently (PETMG F174) from Bed 14 (Hudson & Martill 1994) of the Peterborough Member of the Oxford Clay of the Star Pit near Whittlesey (see Appendix VII) consists of many paired elements (including pectoral fins, preopercles and hyomandibulae) and a significant portion of the branchial basket. Many hundreds of gill rakers were collected and mapped, and this means that a future investigation into variability of gill raker morphology within a single individual will be possible, which might also reveal details of their disposition around the gill basket. It will be noteworthy if any of these retrieved gill rakers display the same white possible mesh structure present in the BMNH P.10000 gill raker (fig. 6.26).

Conversely, the gill raker material described as *Leedsichthys notocetes* seems virtually identical to specimens referred to *Leedsichthys problematicus*, with three caveats: i) the suprafanuncular mesh (which there is evidence for the presence of in Callovian *Leedsichthys problematicus* gill rakers (fig. 6.9C)); ii) the presence of fenestrae, which appear to be an erosional artefact (fig. 6.18A); iii) the degree of internal resorption within the gill rakers (fig. 6.21), which seems more advanced than in other gill rakers examined (see Chapter 7) but this may well be an extension of the pattern of resorption in gill rakers

already noted elsewhere. This material is therefore probably referrable to *Leedsichthys problematicus*, subject only to preparation of associated material revealing real skeletal differences to that taxon.

Removal of the character of presence/absence of gill raker 'needle teeth' did not harm the linkage between *Asthenocormus* and *Leedsichthys*, indeed the introduction of 'Taxon 13' linked all three taxa together in 100% of the most-parsimonious trees.

Chapter 7

"But in this case...the appearance was rather as if the blood had insensibly dissolved and washed away the substance of the Bone, making greatest havock on the softest part of the Bone, as we see in stones of unequal texture that have been long washed by a dropping, or a stream of water. Has the blood that property which some have ascribed to it, of dissolving bony matter?"

William Hunter, 1757

"...he ascertained...the readiness with which the materials of bone are absorbed...and from these facts, laid it down as an established principle, that the absorbents are the agents, by means of which the bones, during their Growth, are modelled as it were, and kept of the same shape."
"Bones, according to Mr. Hunters doctrine, grow by two processes going on at the same time and assisting each other; the arteries bring the supplies to the bone for its increase; the absorbents at the same time are employed in removing portions of the old Bone, so as to give to the new the proper form. By these means the Bone becomes larger, without having any material change produced in its external shape."

John Hunter, 1772. Recalled by Everard Home 1798

"Love to prove it was that big, wouldn't you? Get your name in the National Geographic..." Larry Vaughn, Mayor, Amity Island
"Size isn't everything," says Liston. "Or is it?"
Chris Sloan, National Geographic, September 2004

Chapter 7

Growth, age and size of the Jurassic pachycormid *Leedsichthys problematicus* (Osteichthyes: Actinopterygii).

7.1 - ABSTRACT

The Jurassic pachycormid osteichthyan *Leedsichthys problematicus* is renowned for having been able to achieve prodigious size for a bony fish. Building on Martill (1986a) a thorough examination of all known material was conducted, in order to constrain estimates of the size of this animal, and examine its rate of growth. Important specimens of *Leedsichthys* are described for the first time. The histology of *Leedsichthys* is reviewed, and the presence of growth annuli is used as a tool to establish ages for five assessed specimens. Growth rate analysis is carried out, and correlation attempted between size estimates and calculated ages. Sizes for the five individuals range from 8.0-16.5 metres for ages of 21-45 years, which compare well with length-at-age estimates for basking sharks and whale sharks.

7.2 - INTRODUCTION

The pachycormid *Leedsichthys problematicus* (Osteichthyes: Actinopterygii) has been recognised as an unusually large bony fish since it was first described (Smith Woodward 1889b). It is known from the Callovian of England (Peterborough, Christian Malford), France (Normandie), northern Germany (Wiehengebirge), the Oxfordian of Chile (east of Antofagasta) and the Kimmeridgian of France (Cap de la Hève) (see Chapter 4). Although its osteology has remained poorly known, owing to fragmentary remains and a sparsely ossified skeleton giving it low preservational potential, it has been claimed to be the largest ever bony fish (Martill 1986a). However it is important to be cautious of inadvertently creating giants of mythical proportions (Fortelius & Kappelman 1993), where the slightest misidentification of scant fossil remains can result in significant differences of estimated size in extinct animals (e.g. Liston 2004b).

As a large suspension-feeding fish (Liston 2004a, McNeill Alexander 1998), *Leedsichthys* represents a significant ecological indicator for the levels of productivity in the Oxford Clay sea. In an attempt to quantify this productivity, a series of scaling exercises were carried out (building on the efforts of Martill 1986a), using a variety of remains of *Leedsichthys* and other members of the Family Pachycormidae to estimate likely lengths of this fish. In the absence of a complete specimen which can be measured from the tip of its snout to the base of its caudal fin, it is still possible to estimate the size of *Leedsichthys*

problematicus by scaling individual elements from another fish (preferably of a similar length and from a closely related taxon, to constrain any allometric distortions as much as possible). A histological analysis of bony remains of *Leedsichthys* was then conducted in order to estimate the rates of growth of specimens.

7.2.1 - Pachycormids and Non-Ossification of Skeletal Elements

The phyletic trend across the pachycormids is towards reduced skeletal ossification with taxa of increasing adult size. This is particularly evident in the meristic elements, as vertebral components reduce from being fully present in small adults of *Haasichthys* (Delsate 1999), to only vertebral arches being present in *Hypsocormus* (Goodrich 1930), to sections of the vertebral column only being partially present in *Pachycormus*, only posteriorly present in other members of the Family, and finally absent in *Saurostomus*. The possibility of further reduction, in terms of the absence of pleural ribs, is hinted at by other large specimens (e.g. *Ohmdenia multidentata* Hauff 1953 and an unidentified *Pachycormus* specimen 850mm long, which may yet prove to be an undescribed species Hauff & Hauff 1981: p.80). In addition, the loss of some dermal skull elements in *Saurostomus esocinus* has already been documented (Smith Woodward 1916). *Leedsichthys problematicus* exhibits the preservation of discrete areas of its body suggesting a further loss of ossified elements, mirroring the Cretaceous pachycormid *Protosphyraena*, where only select clumps of its body are found, despite its apparent prodigious size, based on a 685mm span isolated tail (McClung, 1908). It is plausible that, as with other apparently paedomorphic traits within the pachycormids in general and *Leedsichthys* in particular, this occurred through heterochrony within an evolutionarily conserved ossification sequence (Mabee 2000).

As a trend, the non-ossification of skeletal elements is not as problematic for fishes as for terrestrial animals. Support of body weight is not generally a primary function of the skeleton in fishes (Berrios-Lopez *et al.* 1996): a reduced mass in fishes is more likely to reflect the need to lower moments of inertia, thus minimising the energy required for acceleration and deceleration in water (Biewener 1983a), as witnessed in dolphins (de Buffrénil & Mazin 1990). Although Webb & de Buffrénil (1990) have suggested that there would be less need for this reduction in overall skeletal mass in larger aquatic vertebrates, as their need for higher manoeuverability is constrained by their prey choices ("culminating in filter feeding", Webb & de Buffrénil 1990), this ignores the limitations on sub-Teleostean groups (Arratia 1999) (Smith Woodward 1916) such as pachycormids: the potential lack of a gas-bladder (an organ often cited as a specifically teleost character –

Freedman & Noakes 2002) would require significant work against the force of gravity for extremely large sub-Teleostean fishes that had to feed near the surface of open water. As such, any means of reducing concomitant buoyancy problems associated with the development of large size (as well as the need for reduction of acceleration resistance) including the reduction of overall skeletal mass by having a higher proportion of the skeleton as cartilage rather than denser bone, is likely to have been favoured.

7.3 - MATERIALS & METHODS

The majority of the remains of *Leedsichthys* consist of fragments of dermal bones, gill rakers and ceratobranchials. However, some remains contain more useful comparative elements for giving indications of the size range that this animal might have attained, and of these, three specimens preserve discrete sections of its body in an apparently *in vivo* fashion: BMNH P.10000 (the 'tail' specimen collected by Alfred Leeds in 1898, Liston & Noè 2004); BMNH P.10156 (the 'gill basket' specimen, collected by Alfred Leeds in 1905); PETMG F.174 ('Ariston', the specimen collected by Liston, Dawn, Martill *et al.* in 2002-2003, see Appendix VII/Liston 2006). This last specimen, acquired through the financial support of the Palaeontological Association and other contributors, contains a complete and intact pectoral fin. Although not yet fully prepared out, field data for this specimen provides valuable insights into size that aid understanding of the pectoral fragment associated with the 'Tail Specimen' (BMNH P.10000).

7.3.1 - BMNH P.10000 - the 'Tail Specimen':

This specimen consists of the tail of the animal, a fragment of its pectoral fin, and a variety of gill rakers and skull elements. The tail itself consists solely of fin-rays, with no elements from the caudal peduncle or urostyle apparently surviving. As Alfred Leeds appears to have collected this specimen with great thoroughness, and most of the delicate structures of the proximal extremities of the caudal fin have remained intact, it seems unlikely that these elements survived but were separated from the carcass *post mortem*. Instead, it seems most likely that the elements simply were not ossified and thus were not preserved. Support for this is provided by the absence of any urostyle elements from all other *Leedsichthys* remains.

Transported to the British Museum (Natural History) in March 1899, the caudal fin was put on public display shortly afterwards (Liston & Noè 2004). The board that it was mounted on featured a painted background that indicated some of the missing elements – for example, Alfred Leeds recorded that he was unable to retrieve the smaller distal

extremities of the branching rays (Leeds 1956, Liston & Noè 2004), and these were included in the reconstructed background. Similarly, the inter-lobe space was included in the background, with the hypural plate depicted. This area would presumably have been covered by the *interradialis* muscle (Winterbottom 1974). The fin consists of two discrete lobes, but it is not apparent which is the upper and which the lower. In the following description, the terms 'upper lobe' and 'lower lobe' will be used to distinguish between the lobes as historically displayed, rather than indicating an anatomical interpretation of the components as dorsal or ventral elements.

The maximum width (perpendicular to the rays) of the upper and lower lobes is 550mm and 500mm respectively, and their lengths are 1500mm and 1460mm. The lobes are mounted juxtaposed to each other in a fashion that approximates the position in which they were found (this interpretation is based upon a sketch made by Alfred Leeds during the period of excavation, see Liston & Noè 2004). As such, it is valid to note the distances that these lobes would occupy as part of a functioning caudal fin: the horizontal extent of the upper and lower lobes are 1020mm and 1090mm respectively, and their vertical extent is 1230mm and 1140mm. Each lobe is made up of a left and a right half, each consisting of a series of bifurcating non-segmented rays or lepidotrichia. The lack of segmentation is a distinctive feature in the caudal fins of some pachycormids (e.g. the Tithonian *Asthenocormus*, a Toarcian pachycormid specimen SMNS St.12576, and a Callovian pachycormid from the Oxford Clay BMNH P.61563), but not all. These lepidotrichia lie in clusters that may be preservational or excavational artefact, but are a convenient way of breaking down their structure into 5 separate components for the purposes of description: anterior section, mid-section I, mid-section II, mid-section III and posterior section (fig. 7.1). As both lobes are extremely similar (Lambers 1992, Arratia & Lambers 1996), it is proposed that only the lower lobe is described in detail, and this description is also taken to be a reasonable reflection of the other lobe.

Viewed from the subcircular (<5mm diameter) proximal ends of the lepidotrichia, the rays are clearly fused together. In life, these would have been covered anteriorly by the flexors *ventralis* and *dorsalis*, and posteriorly by the *hypochordal longitudinalis* (Winterbottom 1974). These fused rays give the appearance that they lie six deep as a stack of flattened structures, but there are only two layers (left and right) with rays forming a 'pseudostratified' effect when they overlie each other. Initially the rays, thirty eight in number, are 15mm wide with a fasciculated appearance of striations, as though many smaller rays have become fused proximally. In the anterior component (rays 1-6, fig. 7.1),

after the first 230mm, this appearance gives way to a more rationalised quantity of visible units 10mm wide with less striations, and the appearance of a stack of flat rays starts to change to a ray of subcircular cross section. This anterior component is just over a metre in length, with no apparent bifurcations preserved. Mid-section I (rays 7-11) is around a metre in length, and the rays lose their fasciculated appearance around 320mm further down the length of the lobe, bifurcating at 840-940mm. There is one callus growth present on one of the rays. In mid-section II (around 1560mm long), the rays are often laterally paired, with a 'knitting needle' thickness (Leeds 1956) at their proximal origin. They lose their fasciculated character around 215mm down their length (just prior to a large presumably excavation-related horizontal mark across the lobe), changing from a rounded rectangular cross-section prior to their first bifurcations (which take place around 1100-1260mm down the ray), each ray bifurcating a total of 2 or 3 times. Again, there is one callus growth present on one of the rays. Mid-section III (985mm long) has a proximal origin with a 20mm thickness of well-defined fasciculati, which taper over the subsequent 450mm to only 10mm in width. These rays then continue for a further 340-370mm until they bifurcate, and only do so once. There are four callus growths present in this component. In the posterior component (960mm total length), the structure more resembles that of 'unworked plasticine' in appearance – rather than bundles/fasciculati, these rays are more like triangular planar sheets that taper over 485mm, from 30mm wide to 15mm wide. By 310mm down the length, the rays have lost their 'plasticine' and striated characteristics. Each of the seven rays has a bone repair callus at its distal end, and only the first two rays have a single bifurcation (the rest of the rays are devoid of such divisions) at 550-560mm down the component's length.

The total height of the fin (or the span of its trailing edge) is 2740mm, with a surface area of 1.745m^2. This means that the tail has an aspect ratio of 4.32, which is moderately high (Vogel 1994) indicating an animal with a steady cruising speed. Its shape and rigidity (absence of segmentation) also suggests that the fish moved in a 'thunniform' mode. This has implications for the animal's lifestyle that will be dealt with elsewhere (see Chapter 9).

7.3.1.1 - BMNH P.10000 - Pectoral Fin fragment:

This section of the 'Tail Specimen' has recently benefited greatly from the conservation work of Melissa Gunter, working with the Palaeontological Conservation Unit of the Natural History Museum (London) (Gunter 2005). The fragment is 750mm in length, with a maximum width of 235mm (fig. 7.2). Antero-distally, there is much degradation of the specimen due to clay shrinkage, making observations difficult, but it is clear that this slab

does not hold either ray origins or ray terminations. Overall, rays seem parallel until about 400mm down the slab, when the rays appear to bend slightly at an angle of around 10 degrees, to travel more posteriorly, presumably indicating a bend in the fin.

At its proximal end, the fin fragment has ten rays, which proceed distally across the slab without segmentation (as per the caudal fin). Again, these rays appear to occur as a double (superior and inferior) layer, although it is conceivable that each simply represents one ray that has bifurcated around a horizontal plane at a more proximal point to the body than represented on this slab. All rays display rugose striations, with particularly pronounced ornamentation for the first 440mm of the length of the slab. This ornamentation becomes more evident moving from the leading towards the trailing edge of the pectoral fin fragment, the striations growing in relief until they resemble etched, incised or elevated laminae by ray 9. This reflects a change from circular rays (in cross-section) to more flattened rays (initially supero-inferior flattening, then antero-posterior flattening). From the proximal leading edge to the trailing distal point there is a trend towards rays with circular cross-section. The presumed leading edge of the fin fragment is more robust than the more posterior rays. The first four rays are no longer than 190mm, and exhibit no trace of bifurcation. After the first 60mm, ray 5 bifurcates once before extending for the rest of its 340mm – at this point the specimen becomes hard to interpret, due to degradation of the block. There may be a second bifurcation 140mm further down, but a 350mm long ray straddles the 5^{th}-7^{th} rays (and their subsidiary bifurcations), and obscures what might be the origin point of the ray that emerges on the other side. This ray might also be derived from the underside ray, lying in a slightly twisted position.

Ray 6 bifurcates 70mm down its length, again at 300mm and again at 500mm. Ray 7 bifurcates 120mm down its length and a further 350mm on it bifurcates again. Ray 8 bifurcates 100mm down its length, and again at 410mm. Ray 9 bifurcates 230mm down its length. Between rays 4 and 5, at the base of the overlying ray, is a hybodont tooth – a possible indication of post-mortem scavenging activity on the carcass (fig. 7.3).

7.3.2 - PETMG F.174 - 'Ariston':

The above fragment can usefully be compared with field data from the recently collected pectoral fins of 'Ariston' (PETMG F.174). Both fins were found lying as though disposed *in vivo*, and separated laterally by 1005mm of clay (fig. 7.4). The width of the animal's body is likely to have been significantly greater than this (given lengths of individual ribs of more than 700mm), so it is likely that the pectorals were slung below the mid-height

level of the body, as would be expected. The fins are yet to be prepared out from the clay for full examination, and although the leading and trailing edges are apparent, it currently cannot be ascertained whether they are lying upside down or the right way up. They will, however, be regarded as though they are lying the right way up – thus (following the interpretative scheme of Martill 1986b) the putative left pectoral fin unfortunately had a structural slip running through it prior to excavation, causing significant damage, and making precise size estimations exceedingly difficult. The putative right pectoral fin does not have this flaw, and it can be shown to have a length of 1363mm. Through careful examination, the equivalent portion to the fragment represented within BMNH P.10000 can be identified, and a common traverse line (one that crosses 18 rays) used. Comparison of the traverse line in the portion of each specimen shows a fin-width of 278mm at this point in PETMG F.174, and 299mm in BMNH P.10000. If these dimensions can be taken to reflect uniform differences between the two specimens in life, then this would suggest that 'Ariston' is likely to have been the shorter (and possibly the younger) of the two specimens.

7.3.3 - BMNH P.10156 – the 'Gill Basket Specimen'

As a specimen, this will be dealt with in more detail elsewhere (see Chapter 5). A brief description will suffice here for the purposes of scale.

The gill basket is a single specimen sold by Alfred Leeds to the British Museum of Natural History on the 22nd July 1905 (as part of a batch of material bought for £150) (fig. 7.5). It consists of several isolated lumps of clay containing lengths of fin-rays (probably pectoral), a hyomandibula of 870mm length, and the bulk of a gill basket with some opercular elements. Owing to its preservation within a concretionary nodule, all the elements excepting the hyomandibula and the fin-rays can be placed in their original unexcavated position, and indeed the bulk of this latter material made up a single display item in the fossil fish gallery of the British Museum (now the Natural History Museum, London) from around 1905 until 1987 (fig. 7.5). The gill basket consists of both hypohyals, a left hypobranchial I, both hypobranchial IIs, both 810mm long ceratobranchial Is, both 950mm long ceratobranchial IIs, both 990mm long ceratobranchial IIIs, both 940mm long ceratobranchial IVs, and the 340mm long basibranchial IV. Combined with the fused arch V, they produce a gill basket 1140mm wide and 1545mm long.

7.3.4 - Other Material

In order to supplement the above three significant specimens, a series of others are included, to different degrees, in the subsequent series of analyses.

7.3.4.1 - GLAHM V3363 – 'Big Meg'

This represents the most extensive series of remains of *Leedsichthys* to be fully excavated, and was sold to the Hunterian Museum, University of Glasgow in January 1915 (Liston 1999, 2004a) by Alfred Nicholson Leeds (the discoverer of the fish). This specimen features a remarkable diversity of bones amongst its 904 parts, and is particularly useful in having some large skull bones that can be used for establishing a rank order amongst a wide range of other specimens.

7.3.4.2 - BMNH P.6921 – the Holotype Specimen

The holotype also has a wide array of skeletal elements (1,133 parts), of particular use for thin-sectioning.

7.3.4.3 - BMNH P.11823 – a Juvenile/Sub-adult Specimen

An important specimen for its reduced size of skeletal elements, indicating a likely sub-adult or juvenile. This specimen does not include gill rakers, but has some possible lepidotrichial elements, as well as some skull elements useful for establishing a rank order.

7.3.4.4 - The Wallücke *Leedsichthys* Specimen

Erroneously interpreted as a plant and then a stegosaurian dinosaur, this specimen consists of a wide range of material, under a range of collection numbers, held mainly by the Westphalisches Museum für Naturkunde in Münster (see Chapter 4). It has been sampled and sectioned a number of times (e.g. WMfN P.20238) since its discovery in 1983.

7.3.4.5 - Vaches Noire Material

Images of Callovian *Leedsichthys* material sectioned by Bardet *et al.* (1993) have also been used in a review of the histology of this animal.

7.4 - ESTIMATING THE STANDARD LENGTH OF *LEEDSICHTHYS*

7.4.1 - Relative Size

Trying to estimate the Standard Length (SL, *sensu* Holcik *et al.* 1989) from such isolated components is difficult, and it is hoped that the task will be rendered easier when the specimen PETMG F174 ('Ariston') is fully collected and prepared out of its matrix. In the

interim, it is appropriate to make comparisons with the above described partial remains, and relate them to other large pachycormids for indications of how these remains might scale to the SL of a specimen of *Leedsichthys*. In this regard, Martill's original work (1986a) utilised a two metre long pachycormid that had recently been retrieved from the Oxford Clay to scale from, although Patterson (1983) had remarked on its unusual braincase length relative to its body length, and Martill (1991) later noted its "disproportionately small" tail for the length of its body. Although the largest pachycormid fish belong to the genus *Asthenocormus* (adult specimens with a SL of 1.9-2.1 metres are known from the Solnhofen Limestone of Germany (Tithonian)), they will not be used, as few bone morphologies of *Leedsichthys* can be recognised in specimens of this taxon. In contrast, *Saurostomus esocinus* (a taxon from the older Toarcian Holzmaden shale of Germany, for which specimens of as much as 1.7 metres SL are known) does display recognisable forms of bones seen in *Leedsichthys* (Liston 2004a, Smith Woodward 1916), so this taxon will primarily be used for comparison and scaling purposes.

Which measurements should be used to scale for the Standard Length of *Leedsichthys*? Given the large size of many of the remains, the complete absence of any teeth that might belong to the fish, its edentulous jaws and highly developed gill rakers (Smith Woodward 1890b), it would seem likely that this fish was a suspension feeder (Diamond 1985, MacNeill & Brandt 1990, Webb & de Buffrenil 1990, McNeill Alexander 1998, Batty & Domenici 2000, Webb & Gerstner 2000). In this case, it is equally likely that some specialist adaptations took place within the skull to facilitate this lifestyle. Sanderson & Wassersug (1990) noted a tendency in large ram suspension-feeders like baleen whales and the three large suspension-feeding sharks (*Megachasma*, *Rhincodon*, *Cetorhinus*) to have skull lengths that were 25-28% of their Standard Length, but the total skull shape and length are unknown for *Leedsichthys*. In addition, Emerson & Bramble (1993) have noted the marked negative allometry of skull elements with respect to body size even among very closely-related taxa. In such a potentially large vertebrate as *Leedsichthys* it would seem wise to eschew skull components in any exercise of size estimation on the basis that they can be unreliable data sources for scaling. The wisdom of this course of action is underlined by the results of Martill's original work (1986a), which produced figures of 27.6 metres and 13.5 metres from the same specimen of *Leedsichthys* (BMNH P.10156), depending on whether one scaled from the width of the gill basket, or the length of the hyomandibula[i], respectively. A likely explanation for such a striking difference in estimates, is that the gill basket of a fish bears the respiratory surface of the gill filaments – effectively a two dimensional surface, whose square will vary with the cube of the mass of

the body (or the volume of the blood to be oxygenated) that it has to supply with oxygen (Matthews & Parker 1950): this would lead to an animal with a disproportionately large gill basket for the length of its body, as numbers of lamellae are increased (Hughes 1984), as extending the length of the gill filaments does not make a significant difference beyond the first 2-2.5mm (Freedman & Noakes 2002). As Pauly (1994b) puts it: "gills cannot grow as fast as the body they have to supply with oxygen because a surface, even when growing with a strong positive allometry, cannot keep up with a growing volume..."

On this basis, if one restricts the selection of skeletal components for scaling to postcranial elements alone, then one can perhaps be more confident of the accuracy of the resulting estimated length. However, one then has the problem of finding elements that are identifiable both in partial disarticulated remains of *Leedsichthys*, and also in intact well-preserved pachycormids.

This is a particular problem for the 'Gill Basket Specimen' (BMNH P.10156), which features no postcranial material whatsoever (other than fragments of incomplete fin-rays). However, it does feature one of the more ubiquitous and robust elements within *Leedsichthys* skeleton, the hyomandibula. The length of this bone, although perhaps not reliable as a direct reference for scaling, should give an indication of relative size between different specimens of this animal. When broadened to include other skull elements (the ceratohyal[ii] and preopercle[iii]) across the sample group, the Gill Basket (BMNH P.10156), Holotype (BMNH P.6921), Big Meg (GLAHM V3363), Tail Specimen (BMNH P.10000), Ariston (PETMG F174) and 'subadult' (BMNH P.11823) specimens fall in decreasing order of relative size (see Table 7.1).

7.4.2 - Absolute Size

To produce estimates of absolute Standard Lengths, greater emphasis has to be placed on specimens other than the 'Gill Basket Specimen', i.e. those with postcranial elements that can be scaled from. The Glasgow specimen GLAHM V3363 ('Big Meg') has an extensive series of meristic elements, including ribs, anal fin supports and proximal radial supports for the dorsal fin. Taking the longest element of each type, and comparing it with the Stuttgart Museum's 1775mm SL *Saurostomus* specimen (SMNS St.56982) produces Standard Length estimates of 11384mm, 13306mm and (taking the base rib width to the centrum as an estimate of vertebra to vertebra length) 14863mm.

This last estimate was discounted, as pleomerism (the tendency for fish species with larger adult size to have more vertebrae than related equivalents, Lindsey 1988) has often been cited as a mechanism by which bony fish grow to particularly large size in a given family. The concept of pleomerism is based on the idea that within any one body plan there is an optimal segment number, but that this number changes with body length. Williston's Law and Dogiel's Principle of Oligomerization both note the general phyletic tendency for segment number to decrease in fish in general, and increase by Jordan's Rule in polar fish, but increase in larger forms by pleomerism – an increase in vertebral number. Lindsey (1975) noted this phenomenon to be detectable in 90 out of 118 fish families studied. In fact, not only does Lindsey state the Pleomeristic Rule that among related taxa the number of segments is correlated with characteristic body size, but that this relationship is particularly extreme in those fish groups having less complete ossification of the vertebral column, which has been established earlier as a characteristic of *Leedsichthys*. Although it is not possible to determine whether or not pleomerism occurred in the development of *Leedsichthys*, it clearly introduces a further factor of uncertainty that could increase the error margin for any estimate generated.

As the other two estimates come from very differing postcranial elements, and give estimates less than two metres apart, an average figure of 12345mm will be used for the Standard Length of this specimen (GLAHM V3363).

For the 'Tail Specimen' (BMNH P.10000), the lengths of individual caudal lobes (as used by Martill 1986a) and the tailspan can be used in conjunction with the Stuttgart *Saurostomus* specimen, and estimated lengths of 8991mm and 8836mm result. Given that the 'Tail Specimen' had a significantly shallower ceratohyal depth than 'Big Meg', it is not surprising that these results are lower than those for 'Big Meg'. Although both these estimates arise from the same skeletal component (and it is therefore perhaps unsurprising that they lie so close together), an average figure (8913mm) will again be used for the estimated length of this specimen.

For 'Ariston', comparison of the length of the pectoral fin with the Stuttgart *Saurostomus* specimen results in an estimated Standard Length of 8046mm. This is consistent with the size ranking established from comparison of hyomandibulae, preopercles and ceratohyals (see Table 7.1), and with the comparison between the right pectoral fin of Ariston and the fin fragment of BMNH P.10000.

7.4.3 - An Independent Constraint on Size

Liston & Noè (2004) reviewed historical documentation relating to the 'Tail Specimen' (BMNH P.10000), including an account written by Alfred Leeds (in a letter to Arthur Smith Woodward) of the unexcavated specimen, reported as though at least some of the postcranial parts of the animal had been found approximating a life position. Alfred Leeds refers to two fins lying just behind the head and that "back some 12 or 18 feet was found the tail". This has particular relevance to the current study. Although Leeds did not give an interpretation of the two fins, a part of one of them was purchased as a pectoral, and he declares in the letter that he did not believe that he had found the dorsal fin of the specimen. Pelvic fins are rare in large pachycormids – the one metre long *Orthocormus* is the only exception (Lambers 1988). If the pelvic fin is omitted from consideration (no bones related to the pelvic fin have ever been reported or collected for *Leedsichthys*), this leaves two possible interpretations of his words – that the two fins are both pectorals (he stated only that they are 'a good distance apart' without specifying if the separation is related to the width of the animal or its length), or that one is a pectoral and the other is the anal fin. Leeds' letter indicates a distance between the 'last' of these fins and the tail as "12 or 18 feet" – a range of around 3.5-5.5 metres. It seems reasonable to use an average figure for this distance of 4.5 metres. In large pachycormids, the post-pectoral distance is between 73% (for the largest specimens) and 80% of the Standard Length, and the post-anal fin length is 32 (for the largest)-42% of the SL. If the distance quoted in the letter refers to the distance between the pectoral fins and the caudal fin, then a range of sizes of roughly 6164 - 5625 mm is suggested. If the distance referred to is the distance between the anal fin and the caudal fin, then the range of sizes suggested is 14062 - 10714mm. Combining these two ranges gives a minimum and maximum estimated length for the Tail Specimen as found, to be 5625mm and 14062mm. Despite the lack of specific fins being interpreted in Alfred Leeds' letter, these sizes form a range that estimates for the size of the Tail Specimen, should fall within. As such the letter provides an independent coarse check on the validity of estimated sizes, and both estimates (derived above from measurements of the tail) for the Standard Length of the 'Tail Specimen' fall not only within this bracketed size range, but close to the centre of it.

7.5 - CALCULATION OF AGE AND ESTIMATION OF RATE OF GROWTH IN *LEEDSICHTHYS*

With some estimates for the Standard Lengths of a number of specimens of *Leedsichthys*, it would be useful to determine how quickly the animals achieved these lengths, in order to make assessments of their metabolism, and the primary productivity required to sustain

their rate of growth. Despite there being limited remains, the presence of skeletal growth marks in the remains of *Leedsichthys* (Liston *et al.* 2005) enable some age estimations to be made, that can be compared with the sizes estimated above.

7.5.1 - Occurrence of Marks of Skeletal Growth in the Oxford Clay

Skeletal growth marks are produced by internal rhythms, which may become synchronised with and/or reinforced by seasonal environmental cycles, but they are not in themselves indicators of seasonality (Castanet *et al.* 1993). Such marks have been well-known for some time in the Callovian (Middle Jurassic) Oxford Clay, with crocodilians (*Steneosaurus* and *Metriorhynchus*) recording such marks clearly in their teeth (fig. 7.6, fig. 7.7).

In February 2001, the presence of apparent growth increments on some of the bones of *Leedsichthys* was noted, and subsequent work (Liston *et al.* 2005) distinguished between different types of growth bands in different bones of this taxon, revealing the presence of annuli in cross-sections of gill rakers and lepidotrichia. The discovery, later in 2001, of a new specimen of this animal (PETMG F174, 'Ariston', collected over the following two field seasons thanks to significant funding from The Palaeontological Association, Dawn 2004) has resulted in a useful source of experimental material for further sectioning.

7.5.2 - Distribution of marks of skeletal growth in *Leedsichthys* and other fish

Dutch naturalist Thonis Philipszoon (Antonie van Leeuwenhoek) was the first to notice in 1684 that there was a connection between the age of fish and the number of rings of growth on their scales (specifically, on an eel - Leeuwenhoek 1685). The Swedish clergyman Hans Hederström (1759) first recognised growth marks in the bones of bony fish (osteichthyans). Since then, with increasing levels of support from the fisheries industry, researchers have recorded their occurrence in for example cleithra (Casselman 1974, Beamish & McFarlane 1987, Casselman 1996), opercula (Frost & Kipling 1959, Nikolsky 1963), vertebral centra (Welden *et al.* 1987, Newbrey & Wilson 2005, Goldman 2006), fin-rays (Beamish 1981, Burton *et al.* 1999) and fin spines (Holden & Meadows 1962, McFarlane & Beamish 1987), all of which (with the exception of vertebral centra) are certainly present in *Leedsichthys*. In order to estimate the age of its fish populations, the fisheries industry has focussed its growth mark work into analysis of otoliths (Messieh *et al.* 1987) and scales. However, otoliths (it is generally the sagitta/sacculith that is used, as it gives far more distinct annuli than the lapillus/uticulolith or asteriscus/lagenolith – Das 1994) and scales have many drawbacks and problems (Carlander 1987, Beamish 1987,

Rice 1987, Lentsch & Griffith 1987, O'Gorman *et al.* 1987), particularly in comparison with other bones (Castanet *et al.* 1993). Workers on fossil fish still use scales, branchiostegal rays (Micklich 2002) and otoliths (e.g. Reichenbacher & Sienknecht 2001), but this is precluded in *Leedsichthys*, as none of these components have been identified. In *Leedsichthys*, the marks of skeletal growth occur in the splanchnocranium and the appendicular skeleton.

7.5.3 - HISTORY OF WORK ON GENERAL HISTOLOGY OF *LEEDSICHTHYS*

7.5.3.1 - The Wallücke Specimen:

Thin section analysis of *Leedsichthys* bone was first conducted in 1983 by Martin Büchner of Bielefeld Natural History Museum, in order to resolve a dispute over the nature of fossil fragments that had recently been excavated from the Wallücke quarry in the Wiehen Mountains of northern Germany (see Chapter 4). It had been suggested that the fragments might represent either plant or vertebrate remains. Büchner observed the presence of both compact (fig. 7.8a) and cancellous (fig. 7.8b) bone in the fragments, and so dismissed the argument that the remains represented plant material.

In this image from one of Büchner's original sections, a level of bone growth can be seen that would be unusually high for most fish (Enlow & Brown 1958) (fig.7.8a,b). Significant remodelling has taken place, producing a high density of Haversian systems. Many of the canals have been infilled with sediment (fig. 7.8a; a), and asymmetrical secondary centripetal deposition can be seen, occasionally blocking former reticular channels (fig. 7.8a; b) and indicating more than one cycle of secondary deposition. Near the surface of the bone, there is more evidence of some of the primary bone still remaining between the osteons (fig. 7.8a; c), with superficial resorption from the surface of the bone having taken place (fig. 7.8a; d). In contrast, the image of a detail from an area of more porous cortical bone shows reticular channels unblocked by further bone growth (fig. 7.8b; e). Although it has not been recorded which element this section was taken from (as the initial bones found were described as 'reed-like' in external appearance (see Chapter 4), the element was probably a lepidotrichial fragment), it is clear that it is a bone that underwent a high level of secondary remodelling (Thomason 1995), leaving no trace of any original zones or annuli that may have been present. It is therefore unsuitable for analysis to determine the age of the specimen. This problem has been noted during attempts to count growth rings in other extensively remodelled fossil material (e.g. turtles, Scheyer & Sánchez-Villagra in press).

7.5.3.2 - Vaches Noire Material:

The second time that *Leedsichthys* bones were sectioned was to resolve a different question of identity – although it was recognised that the fragments represented fossilised vertebrate remains, the fragments were unfamiliar to those used to collecting marine reptile remains from the Vaches Noire, Normandie, France. Bardet *et al.* (1993) sectioned what proved to be part of a *Leedsichthys* ceratobranchial, again finding compact and cancellous bone (fig. 7.9). The sectioned element has not retained any traces of the external fibrous bone that would have contained the hypertrophic and growth zones of cartilage (fig. 7.9) (Takashima & Yokote 1995). Under low power, a highly dense network of Haversian systems was revealed, with far less mineral infilling than in the Wallücke section (fig. 7.10A). Even less interstitial primary bone is evident, and no trace whatsoever of any original annuli or zones exists, or any indication whether the primary osteons were laid down in bundles, radial rows or circular rows (Francillon-Vieillot *et al.* 1990). The vascular canals are not strictly longitudinal, as they mostly show signs of travelling at angles varying slightly from perpendicular to the plane of sectioning (fig. 7.10B), which creates the effect of drift in centripetal deposition within the osteon. In crossed polars, the fibrolamellar constitution of the secondary osteons becomes clear (fig. 7.10C). In the section showing the spongy cortex (fig. 7.11A), the bony framework appears more slight than in the Wallücke section, with fewer lamellae going to make up supporting 'struts' of the trabeculae around the intertrabecular spaces (fig. 7.11B). Bardet *et al.* (1993) reported that the cortex around the medullary cavity had been subjected to intense remodelling, with signs of repeated erosion and reconstruction, and annuli indicating cyclical growth. They interpreted all of these signs as indicating an animal with a "high metabolic level....subject to a certain seasonal fluctuation". Again, although this bone shows signs of annual growth, the level of bone remodelling prohibits its use in estimation of the age of the specimen.

7.5.3.3 - Wallücke Revisited:

A further section (GLAHM 109519) was cut from the Wallücke specimen of *Leedsichthys* as part of a faunal review by Michelis *et al.* (1996), from what appears to be a cerato/epibranchial junction of the specimen (WMfN P.20238, fig. 7.12). Michelis *et al.* (1996) argued that there was no compact bone present on the specimen, and that this could therefore be a means for distinguishing between tetrapod bones and *Leedsichthys* in the future (the two have frequently been confused in previous identifications – e.g. Hulke 1887, von Huene 1901). This is erroneous for two reasons. Firstly, de Ricqlès *et al.* (1991) specifically noted that 'peculiarities' of bone histology cannot be regarded as being taxa-specific evidence with taxonomic significance, and Francillon-Vieillot *et al.* (1990)

explicitly stated that the presence or absence of compacta is not diagnostic of precise anatomical or ontogenetic origins. Further, Francillon-Vieillot *et al.* (1990) noted that marine animals can have particular specialisations, for example, cetaceans lack true compact bone tissue in their flippers. Secondly, there is compact bone present in this section, approx. 0.2mm thick, detectable at the top left of this section (fig. 7.13 and fig. 7.14 detail), bounding an extensive spongy cortex extending to the medullary cavity[iv]. Close analysis of trabeculae surrounding an intertrabecular space reveals marks of skeletal growth (fig. 7.15), but as part of secondary remodelling they will not be of any value in determining the age of the specimen.

It is noteworthy that, although reticular canals have been observed, no trace of Williamson's Canals (Enlow & Brown 1956) have been visible, in spite of this being a typical feature of Holostean bone (de Ricqlès *et al.* 1991). Other than this, the characteristics noted in the images of the sections described above are not intrinsically surprising. As noted by Francillon-Vieillot *et al.*, in long-lived animals most parts of the cortex consists of dense Haversian systems, with smaller animals having simpler patterns with only moderate Haversian substitution restricted to a bone's cancellous region (1990). Bardet *et al.* (1993) noted that the level of secondary remodelling present in their section indicated a high or elevated metabolic level for a fish, with apparent seasonal fluctuations in growth. Although this presents some interesting palaeoecological questions for our further understanding of the Callovian marine ecosystem, it does not, however, augur well for the prospects of being able to detect annuli to aid in estimates of the age of *Leedsichthys* specimens, as secondary remodelling and resorption will have removed the annular rings necessary for reliable age estimation. But, as noted by Castanet *et al.* (1993: p. 261), not all bony elements will record marks of skeletal growth to the same quality (Enlow & Brown 1958, de Buffrénil & Mazin 1990), and in such situations an exploratory survey of the variety of bony elements available is necessary, in order to assess their relative value for skeletochronological examination.

7.5.4 - New sections taken from different skeletal elements

The sectioned examples from Germany and France reviewed above are unusual, in that most specimens of *Leedsichthys* (including the type material) have not come from these localities, but have been found in the brick clay excavated from the neighbourhood of Peterborough, England. One of the common characteristics of specimens of *Leedsichthys* found from this general locality is that they are severely crushed – Arthur Smith Woodward (1889b) noted this in his original description when he referred to a 'diploë' in

the ?skull bones, and given the porosity observed in the sectioned bones above, this is straightforward to understand. The bone simply does not survive the pressure of clay overburden as well as marine reptile bone does in the same diagenetic regime, creating a 'sandwich' effect of two comparatively thin layers of compact bone on either side of a thin intervening layer that represents the crushed and flattened highly porous cancellous bone. This is a ubiquitous problem with bones identified as being part of the dermatocranium of *Leedsichthys*, which are often found with the compact layers having fragmented away from each other. With regard to the detection of annuli, a further constraint of *Leedsichthys* remains from this geographical area, is that thicker skeletal components, such as meristic elongated elements, are frequently fully remineralised internally, leaving no trace of their former histological character. However, more slender elements seem to not be subject to this regime, perhaps by virtue of retaining a denser compacta that resists mineralisation.

This characteristic was observed when fragments on the spoil heap from the 2002 'Ariston' excavation were sectioned for geochemical analysis (Challands & Liston 2003). It was found that gill rakers and lepidotrichia clearly recorded annuli. It appeared that, of the two elements, gill rakers recorded annuli with greater clarity than the lepidotrichia. Both of these elements are comparatively common finds amongst the partial remains of this animal, with gill rakers and/or lepidotrichia occurring in around 50% of the 70 known specimens of *Leedsichthys* (see Appendix IX) and this made any procedure based on these elements potentially one of the widest utility to other specimens. This is important, as many of the skeletal elements of *Leedsichthys* have been recorded from only a very limited number of specimens (e.g. out of over fifty individuals, a maxilla is only known from specimen GLAHM V3363, and a dentary only from BMNH P.66340), and a procedure that was reliant on relatively scarce elements such as these being present, would be of limited value to the vast majority of specimens of *Leedsichthys*.

Gill rakers were sectioned from the specimens used in section 7.4 - 'ESTIMATING THE STANDARD LENGTH OF *LEEDSICHTHYS*' to give estimates of size, in order to compare counts of annuli with sizes estimated. Where possible (and identifiable), lepidotrichial and other meristic fragments were also sectioned, to compare results with the counts visible in the gill rakers. Sections from both types of bones were mounted as polished sections for microscopic examination, photography and analysis.

For full listings of measurements of annuli see Table 7.2.

7.5.5 - Practical problems encountered

It was difficult to establish a rigorously consistent point along a gill raker for a transverse section to be taken from, as gill rakers are rarely found complete, and preference was given to the section presenting annuli with greatest clarity, rather than from a consistent position along the length of the raker. Given this, and the variable size of the rakers within an individual, the dimensions of raker sections taken varied widely.

Determination of a central measuring point for the annuli was also problematic, as with any growth structure that is irregular (e.g. sagittae, in Das 1994) compared to the relatively simple procedure of defining a focus on the external surface of a scale (Matlock *et al.* 1987). An arbitrary central point was used in all cases.

7.6 - RESULTS

The sections presented a series of concentric growth marks, with broad light zones and narrow darker annular bone in reflected light (fig. 7.16-7.22). These marks were identified as annuli rather than LACs (lignes d'arrêt de croissance = lines of arrested growth), as they did not present discontinuities, and were more than double the upper thickness limit of 5 microns for LACs (de Ricqlès *et al.* 1991: p. 38). It is perhaps unsurprising that an animal thought to grow so large would lack this histological character, as size will confer a degree of stability of body temperature to the animal (what is sometimes referred to as 'gigantothermy' see e.g. de Buffrénil & Mazin 1990), therefore full cessation of annual growth would be unlikely, especially once an 'adult' size had been reached.

As the number of growth marks appeared to increase from section to section, so the degree of internal remodelling and resorption appeared to increase within the gill rakers. A high level of vascularisation also posed a problem (in terms of visibility of annuli) within meristic elements of two specimens sampled. However, resorption did not appear to present a significant problem with lepidotrichia sampled.

Full listings of numbers of zones present are contained within Table 7.2, and age and Standard Length estimates are summarised in Table 7.3.

7.6.1 - Description of Polished Sections

'Ariston' (PETMG F174)

Three elements were sampled from this specimen – the lepidotrichium presented 21 annuli, compared to 17 in the gill raker.

The gill raker showed clear signs of remodelling in its centre, with partial erosion of the innermost remaining rings (fig. 7.17), whereas the lepidotrichium did not (fig. 7.16). When sectioned, the meristic element (PETMG F174/264) was found to be extensively remodelled, and unsuitable for use (fig. 7.18).

'Tail Specimen' (BMNH P.10000)

The gill raker sectioned revealed 19 annuli, again with signs of resorption of the innermost annuli (fig. 7.19). Relating the pulses in growth evident in plots for both this specimen (Appendix IV, Graph 3) and the gill raker of 'Ariston' (Appendix IV, Graph 2), and assuming that these reflected a growth surge at a uniform age, it was estimated that around 6 annuli were missing due to resorption in this section.

'Big Meg' (GLAHM V3363)

The meristic element showed only 15 annuli, but around 60% of the core of the element had been resorbed (fig. 7.20). On this basis, comparing it with other meristic elements, it was estimated that around 12-16 annuli had been resorbed.

Holotype (BMNH P.6921)

The lepidotrichial fragment showed 40 annuli (fig. 7.21A), with the gill raker showing 33 (fig. 7.21B), with signs of internal resorption of annuli, as with the other gill raker specimens sectioned.

'Gill Basket Specimen' (BMNH P.10156)

The gill raker showed 37 annuli, with significant internal resorption and remodelling (fig. 7.22). Comparison with the other gill rakers suggested that around 7 annuli had been resorbed.

Both lepidotrichia sampled (PETMG F174, BMNH P6921) displayed signs of a strong early surge in growth. The corresponding gill rakers sampled consistently presented fewer annuli than the lepidotrichia, with signs of internal remodelling and resorption of earlier marks of skeletal growth. Peaks of growth could be matched between each sampled element within a specimen. This enabled counts of 'missing' annuli to be made (see Appendix IV: Graphs 1-7). Similarly, pulses of growth in gill rakers of different specimens were used to infer numbers of missing annuli between specimens, where appropriate.

The sample taken from GLAHM V3363 (fig. 7.20) indicated a highly vascularised bone, with roughly 60% of its core having been resorbed, and only 15 annuli detectable at its periphery. Internal remodelling was even more noticeable in BMNH P.10156, where post-depositional pyrite had developed secondarily, replacing much of the secondary bone, and occasionally appearing down primary vascular canals (fig. 7.22). 38 annuli were still clearly visible in this specimen, indicating that the actual number of annuli laid down during the life of the animal was likely to be much higher. Although these last two specimens lacked a definitive annular count, the levels of internal resorption in their gill rakers were consistent with the initial large estimates made for their Standard Length within the initial group sampled (7.4.2).

7.6.2 - Estimation of Growth Rate from annular growth marks

Previous workers have used the growth of a single skeletal element as being proportional to the rate of growth of the entire fish. Einar Lea (1910) used the length of annuli from the centre of herring scales for that purpose (e.g. Frost & Kipling 1959, Parker & Scott 1965). Lea's work has been taken forward by several workers, with Ludwig von Bertalanffy (1938) being arguably the most significant innovator since then (Pauly 1994a; and see Moreau 1987, Wootton 1991 and 1992 for reviews comparing other growth models, such as Gompertz, Johnson, logistic and Richards).

Following on from the work of Burnham-Curtis & Bronte (1996) and Newbrey & Bozek (2003) on scales and otoliths, that used Lea's (1910) principle that the annual growth of bony structures is proportional to the annual growth in body length, a von Bertalanffy (1938) growth curve was constructed from the polished sections used above to estimate growth rate in the different specimens of *Leedsichthys* examined.

Transects were taken across the polished sections, and the distance from an arbitrary centre to the start of each annulus was recorded. Transects were selected on the basis of passing through the greatest quantity of distinct growth marks, avoiding any areas of remodelling wherever possible. For the purposes of measurement in this study, the interface point between the light zones and dark areas was taken as the point of origin of a new annulus. The distance from this point on the transect to an arbitrary 'centroid' was measured for each annulus, and the results plotted for each skeletal element. Growth curves were then fitted to the data.

Full listings of numbers of zones present and measurements of annuli are contained within Table 7.2, and linear plots of this data are contained within Appendix IV (Graphs 1-7).

7.6.3 - Fits of growth curves

Both von Bertalanffy and linear growth models were fitted to the data. In neither case were the data constrained to run through the origin. Both models gave very high levels of explained variance (linear growth encompassing between 96.4 and 99.7% of the variability in the data), but plotting graphically there was no evidence of a clear maximal size for any of the specimens examined (i.e. there was no asymptote in the bone increment on age plot). This observation is further supported by the very large variances on the values for $L\infty$ estimated using the iterative non-linear regression model (in SPSS – Statistical Package for the Social Sciences), which gave 95% confidence ranges from 0.99-30,399. It was clear that (provided that the growth of these elements are a fair equivalent of the growth of the animal overall) there is no sign of determinate growth within the range of specimens sampled here, as no asymptotic point was determinable, as shown by this large range of L infinity (Pauly 1994a) produced by the data. For this reason, the linear regression model of growth was accepted as an appropriate descriptor for the growth of these specimens over the period recorded in the skeletal elements (fig. 7.23). This was further reinforced when the data was replotted using a Walford-Ford plot (Walford 1946) – the data parallelled the line of unity, giving no indication of an ultimate length for the animal (fig. 7.24). This unfortunately meant that neither statistical method could provide a reasonable estimate of the animal's potential longevity (Das 1994).

In addition, when applied directly to the figures for the estimated sizes of the individual specimens, the gradients derived from the linear plots gave unconvincing intercepts with an exceptionally slow rate of growth (fig. 7.25). The possible significance of this is discussed below.

7.7 - DISCUSSION

7.7.1 - Annuli - realistic indicators of age and growth rate in *Leedsichthys*?

The lack of ossification of elements of the skeleton has been a problem for workers on *Leedsichthys* since it was first fully described (Smith Woodward 1889b). Jørgensen (1966) noted reductions in the skeletal mass of pelagic suspension-feeders and interpreted this as a reflection of the very limited food supply reaching that depth (1,000-4,000 metres) of the water column. Taylor *et al.* (1983) made similar observations with regard to reduced skeletal development of various mesopelagic teleosts and the extremely poor calcification

of the skeleton of *Megachasma pelagios* in its deep water oceanic habitat. In contrast, the Oxford Clay sea has been bracketed as a 50-200m depth epeiric sea (Martill *et al.* 1994), and as one of high productivity. As such this seems to be a strategy that is not dictated by limitations of nutrient supply. But it has no doubt restricted the number of elements that have been preserved with annuli.

Amongst preserved elements, many are remineralised, eradicating any trace of annuli that may have been present. Others which have preserved annuli have had a portion of them resorbed. Resorption of bone has been known as a natural part of bone growth since John Hunter first noted it in 1772 (published posthumously by his assistant Everard Home in 1798). Although the gill rakers contained clear and distinct annuli, they were variably affected by resorption, indicating that these elements were highly vascularised, in contrast to the lepidotrichial fragments examined. Although the lepidotrichial fragments shed more light on the early period of growth, they do not appear to provide enough information to illustrate in detail the first 1-2 years of growth of the animal as a whole.

There are a number of possible explanations for this. The varying abilities of different skeletal components to record the first two years of growth is known in many contemporary fish, and dependent on both when the elements appear and when they ossify (e.g. Casselman 1996). It could also be that neither the gill raker nor the lepidotrichium is a good analogue for the growth of the whole animal, and the growth patterns are solely a dislocated growth pattern for the elements themselves. As Castanet *et al.* (1993) noted, a single section from one bone may not be representative of the skeleton as a whole. Burnham-Curtis & Bronte (1996) made a distinction between otoliths and scales for lake trout, determining that the sagittae provided a more accurate model for the growth of the whole animal. It may be that, although the gill rakers and lepidotrichia are good recorders of annular growth marks, they are not elements of the skeleton that reflect the growth of the whole animal well. Lea (1910) referred to the variability of the results from measurements on different scales depending on the suitability of the scale for estimation of body length, and given the breadth of rates of growth possible through varying the angle of transects through a raker or lepidotrichium, it is clear that absolute estimates of rate of growth must be approached with caution when employing this method.

Alternatively, the elements might be functioning as effective analogues for the growth of the whole animal, but merely lack sufficient resolution of the very early surge in growth. Growth may be linear, curvilinear or sigmoidal (Das 1994). As such, the linear pattern

recorded in the graphs could be the main limb of a sigmoidal or curvilinear growth pattern, or reflect the total linear growth of the animal. The lack of an asymptote (or even the indication of the approach of one) in the growth of any of the specimens, combined with the pattern of consistent but extremely slow growth for all but the first two years of annuli recorded in the thin-sections, makes a sigmoidal pattern of growth very unlikely. If this pattern of linear growth is accurate, then (given that it would predict a Year Zero or hatching size of between 5 and 8 metres – see fig. 7.25) it must only relate to the skeletal element, and not to the growth of the total animal. Conversely, the low rate of growth recorded in these skeletal elements may be accurate for the growth of the animal in the period subsequent to its first year of growth, but rather than reflecting an entirely linear growth pattern, it could instead indicate an extremely fast year 1-2 of growth, as with the rapid postnatal growth noted for marine animals with a thunniform morphology (de Buffrénil & Mazin 1990). Fast growth to large size gives protection from predators, but as Nikolsky (1963) notes, this is only possible in the presence of an abundant food supply, with the associated risk of increased exposure to predators (Helfman *et al.* 1997). Hudson & Martill (1991) and MacQuaker (1994) have both written on the high levels of primary production in the Oxford Clay sea (the epeiric sea environment that the sectioned specimens came from), with a mean organic carbon content for the Lower Oxford Clay (=Peterborough Member, Cox *et al.* 1992) of 5.1%, and a large amount of accumulated organic matter mainly from marine phytoplankton. Casselman (1996: p. 83) has noted that the availability of prey "directly affects the size relations between calcified structures and the body", so might also affect scaling.

In contrast to this, it is noteworthy that the von Bertalanffy growth coefficient 'k' (Pauly 1994a) produced for the plotted skeletal elements from *Leedsichthys* was no higher than 0.004 for any specimen. These figures may of course again simply relate to the growth of the element and not to the whole animal, but in Class Chondrichthyes, sharks and rays grow at a slow rate, with k = 0.04-0.16, tending to live long and attain large sizes, with dogfishes (*Squalus*) having a lifespan up to 70 years (Das 1994). Some actinopterygians can live longer than this (some species of sturgeons live up to 152 years), and although most teleosts have a lifespan of between 2 and 15 years, some species of rockfish can live over 120 years (Das 1994), the estimate for *Sebastes aleutianus* being 205 years (Berkeley *et al.* 2004).

The level of the k coefficient has a further ecological significance. In times of local ecological stress, large animals in oceans are less vulnerable to localised ecological

changes, as they are more able to move elsewhere (e.g. Bakker 1993) in comparison with their smaller (or terrestrial) or fixed faunal counterparts. Musick (1999), in his work on ecology of long-lived marine animals, found that the Von Bertalanffy growth coefficient k was a useful indicator of vulnerability to (and poor recoverability potential from) excessive mortality events. In particular, where k was less than or equal to 0.1, the animals were particularly vulnerable (for example, most elasmobranchs, most chondrichthyans, some teleosts and the cheloniid sea turtles). This was because such animals usually had low fecundity, slow growth and late maturity, in other words a low rate of increase, meaning that their recovery from any excessive mortality event might take decades. Benton (1986) noted similar problems for animals of large size.

In contrast to the apparent problems of deriving a convincing model of growth rate in *Leedsichthys* from these skeletal elements, it is worth trying to independently assess the validity of the method used, in terms of the ages and sizes derived. There is agreement between the sizes of individual bones (in terms of the 'rank' order of likely relative size), and the estimated sizes of the total animals, arrived at independently of those individual bones. Notwithstanding the caveat that individual body size is not always a sound indicator of relative age (Castanet *et al.* 1993: page 269), there is further agreement between the order of calculated age of the specimens, and their estimated sizes. But do these figures for age and size seem biologically realistic?

The natural contemporary comparator animals for *Leedsichthys* are the whale shark, *Rhincodon typus*, and the basking shark, *Cetorhinus maximus*, as both are large pelagic suspension-feeders. There is scant information on the size and growth of the whale shark: most sighted individuals are between 3 and 10 metres in length (Uchida 1983, Clark & Nelson 1997), with the longest individual reliably reported as 12 metres (Colman 1997), although other reasonably credible sources can give higher figures (Compagno 2001). The only estimates for size-at-age relate to the minimum for maturity, being a Standard Length of over 9 metres and an age of over 30 years (Colman 1997). For the basking shark, there is a little more data, with Sims *et al.* (2003) noting its habitat to be primarily up to 200 metres water depth, reminiscent of interpretation of the depth of the Oxford Clay sea (Martill *et al.* 1994). For sizes, Sims *et al.* (1997) notes estimated ages of 3-4 years for a 5 metre long individual, and 8-15 years for 10 metre long individuals, with sexual maturity at 6-9 metres. 11 metre long individuals have also been reported (McNeill Alexander 1998). Plotting these estimates next to those calculated from the foregoing work demonstrates a surprising agreement (fig. 7.26) – the growth rates (in terms of size-at-age data) for each

shark bracket those of *Leedsichthys*, so the figures do not appear to be unrealistically fast or slow when compared with modern-day large suspension-feeding chondrichthyans. As such, once data has been obtained from annuli of younger individuals of *Leedsichthys*, it will be interesting to compare with length-at-age data available for basking sharks (Parker & Stott 1965).

7.8 - CONCLUSIONS

Available specimens of *Leedsichthys* were selected and placed in a likely rank order of relative size, based on the size of cranial elements common to more than one specimen. Careful selection of postcranial elements for scaling resulted in reliable size estimates. Gill rakers and lepidotrichia were sectioned and counts of annuli were used to derive estimated ages for the individuals. All three processes produced congruent results, with the rank order of specimens tallying with the order of the postcranially-based size estimates, which in turn agreed with the estimated ages derived from annular counts. Although examination of further material is necessary for the resolution of growth rate, in particular in the first years of life, this technique has importantly demonstrated a consistent pattern of size and age among different specimens of *Leedsichthys* from three differing areas of their skeletal remains. The size and age estimates are compatible with what is known of the growth of large modern-day oceanic suspension-feeding chondrichthyans.

Although *Leedsichthys* appears to have grown to a remarkable size for a bony fish, its growth, both in terms of rate and extent, is broadly comparable with basking sharks and whale sharks today.

7.9 - Chapter 7, Endnotes

[i] It should be noted that it is unclear which specific element Martill was scaling from – no hyomandibula is apparent from the remains of the fish that he was using, and Martill later (1988) figured the hyomandibula of *Leedsichthys* as a ceratohyal.

[ii] Depth of the ceratohyal was used instead of its length, because the superior and inferior surfaces are more robust and well-defined than the fragile and frequently incomplete proximal and distal ends. In spite of this, only partial remains of the left ceratohyal of the 'Gill Basket Specimen' are preserved, covering the first and second left hypobranchial, so only a minimum (rather than an absolute) value of 84mm could be ascertained for its depth, with an estimation of around 160mm depth based on comparison of the orientation of surface striae with other specimens. If it extended further over the surface of the bones present, it could have been up to 230mm deep.

[iii] Hypobranchials and ceratobranchials were also considered for use in this exercise, due to their reasonably common occurrence within the remains of *Leedsichthys*, but there were two problems that excluded them: firstly they were subjected to variable degrees of crushing, therefore horizontal distances were difficult to measure in a uniform way for all specimens. This introduced a significant amount of error. The second problem, is that no specimen exists for which all the hypobranchials are known, therefore the expected range within the series of an individual is difficult to determine. Similarly, the ceratobranchial series is only known in full for an individual for BMNH P.10156, but the supporting clay would need to be more fully excavated before widths of these tapering elements could be confidently measured. This last element of error meant that neither of these branchial series were used to rank size in specimens, despite their common occurrence.

[iv] It is, however, worth noting that it was unfortunate that Michelis *et al.* (1996) selected a branchial element for sectioning: looking at the histology of living teleosts (e.g. carp), the ceratobranchial has a thin periosteum bounded externally by a layer of fibrous bone which is covered in turn by a thick layer of cartilage with in turn a further thin external layer of fibrous bone (Takashima & Yokote 1995). This means that (assuming the construction of the branchial elements is broadly similar in pachycormids) their selection of this element for sectioning was always unlikely to give them anything more than, at best, an exceptionally thin layer of compact bone.

Chapter 8

"...though we may as philosophers regret it, as men we cannot but thank heaven that its whole generation is probably extinct".

William Hunter speaking on the '*Ohio incognitum*' (1768).

"And nothing can we call our own but death,
And that small model of the barren earth
Which serves as paste and cover to our bones.
For God's sake, let us sit upon the ground
And tell sad stories of the death of kings:
How some have been depos'd, some slain in war,
Some haunted by the ghosts they have depos'd
Some poison'd by their wives, some sleeping kill'd;
All murder'd for within the hollow crown
That rounds the mortal temples of a king
Keeps Death his court."

(From 'The Life & death of Richard the Second', Act III, Scene 2) W. Shakespeare (1595)

Chapter 8

The Osteology of *Leedsichthys*: Beyond the Bone Identifications of Smith Woodward.

8.1 - ABSTRACT

The identity of any bone of *Leedsichthys* that is not a gill raker or a fin-ray has long been elusive, with bones in museum collections frequently only classified as 'skull bones' or '?frontals' if flat, and 'rib-shaped bones' if elongate and curved. Eight years after describing eight bony elements within the type specimen (BMNH P.6921), Smith Woodward noted that he only retained confidence in his identifications of two of those elements. The type material is redescribed, with some elements reidentified, and further bone morphologies within the type material and other specimens are identified. A wide variety of postcranial meristic elements are distinguished and identified, on the basis that their curvature is determined by stress regimes specific to the location of the curved bone within the skeleton.

8.2 - INTRODUCTION

The osteology of *Leedsichthys* has been a problem ever since the material was first identified as worthy of description in 1886 (Hulke 1887). Partly, this problem has been due to the skeletal nature of the animal – the bones are large and fragile, and frequently found in a highly fragmented state. This made it difficult for the original workers to recognise what sort of an organism the remains represented (see Chapter 4), and what the different components were.

But there are also human factors that have provided obstacles. The scientific workplace prefers studies that can swiftly be completed, or done in parallel with other work. *Leedsichthys* has difficulties fitting into this role: the nature of the bones (their scale and fragility) require time and care to reassemble with support and chemical treatment to prevent further deterioration. Having rejected the bulk of his own early identifications (1889b, Leeds & Smith Woodward 1897), Smith Woodward appears to not have had the time to complete his work on BMNH P.10000 to produce the full description of its osteology that he aspired to in his catalogue of fossil fishes (1895, indeed based on the handwritten manuscript in the NHM archives, his work on the supplement to the catalogue does not seem to have progressed beyond the cartilaginous fishes), and this work was sidelined by more hominid interests with the 'discovery' of Piltdown Man (Liston 2004a). The *Leedsichthys* material that he seems to have kept separate from the collections in

office trays (rather than museum drawers, pers. obs.) was eventually incorporated into the collections at the BM(NH), with no memory of its provenance retained within the organisation.

A further problem with the condition of the material arose in January 1972, when the process of moving the BM(NH) basement palaeontological stores to the Waterhouse building resulted in the overturning of a flatbed trolley of *Leedsichthys* material, causing further breakage and mixing of specimens (fig. 8.1). In the midst of such a large scale move of collections, there was no opportunity to stop and sort the material properly. During the sorting of BM(NH) material throughout the course of this current work, elements of at least three specimens (including the holotype BMNH P.6921) were separated from other specimens and reunited with their original components.

Other post-collection breakages have occurred. The bulk of palaeontological specimen damage does not come from environmental problems, but from over-handling (Fitzgerald 1995, Wilson & Currier 2001, Doyle pers. comm. 2004). In Glasgow, the bulk of GLAHM V3363 was damaged by an over-enthusiastic driver bringing the bones to a display space for a television company to film them. In his rush, the driver failed to notice 'sleeping policemen' traffic controllers. The conservation glue employed on the specimen, Paraloid B72, is not shock-resistant, and the work of several years of glue repairs to the 904 parts of that specimen was undone in a moment.

Another museological phenomenon that *Leedsichthys* has suffered from, is that some of its bones are exceptionally large, beyond the size of most museum storage cabinets. This leads to storage problems, with outsize components frequently being separated from components that do fit within conventional storage, even when they are part of the same specimen, and placed in a unique location (e.g. the top of a storage cabinet, where it cannot be seen), the details of which become lost or forgotten over time. This can be a particular problem if the specimen (as frequently true with *Leedsichthys*) consists of many elements that have not all been numbered. A more unusual museological problem that *Leedsichthys* has been subject to, was the generation of unfounded ideas regarding relationships of specimens that can grow within the custodial institution, to the point of misleading labels being publicly displayed (Liston & Noè 2004). A failure to check with original sales documentation and correspondence has resulted in parts of specimens being separated from their correct numbers (Liston & Noè 2004) and from their original identification as *Leedsichthys* (Neaverson 1935).

The bulk of this work is aimed at completing Smith Woodward's stated objective (1895), of producing a review of this animal's osteology when new material became available, both by assessing his original identifications, and by identifying further bony elements. This has largely been achieved without reference to the recently excavated Star Pit specimen 'Ariston' (PETMG F.174), because there are so many bones of this specimen that still await preparation from their plaster jackets, or require to have their protective casing of Paraloid B72 glue removed. However, personal observation of the bones of this animal throughout their uncovering and retrieval has informed this assessment. This work does not place great emphasis on material not recovered from Peterborough's Oxford Clay, because the north German material is (apart from fin-rays and the hypobranchial) extremely difficult to distinguish from its matrix, the French material consists (with the exception of some exquisitely preserved gill rakers) of isolated fragments and the Chilean finds are embedded in such a hard limestone that the material is scattered through many hundreds of fragments of matrix and impossible to work on without further extensive preparation. Any osteological identifications that have been made based on non-Peterborough material are noted within the text.

The work on BMNH P.6921 involved a large amount of repair and reassembly, which over the years reduced the number of parts in the specimen from 1,133 to 862. However, there is still a large quantity of fragments that have not been located on their original bones, and as will be seen in the following descriptions, some of Smith Woodward's original bones appear noticeably incomplete when compared with his recorded measurements of 1889 (1889b). The incident with the flatbed trolley in 1972 is probably a major factor in this regard, although Hulke's (1887) dimensions are noticeably larger than both the flat bones that Smith Woodward describes, implying that some loss of material had already occurred by the time the primary description was made (Smith Woodward 1889b).

In contrast, when PETMG F.174 is referred to, it is worth noting that exceptional care was taken to lift the bones of this specimen, and conservation glue was applied so that virtually all of the bones were coated with a protective shield while they were still in the clay prior to them being lifted, so that they were retrieved in as few fragments as possible. This methodology was born from the knowledge of the extreme fragility of the fossil remains of this animal, and how rarely perimeters of the bones are preserved amongst the hypodigm of known specimens today. This method was not available to Alfred Leeds, and as a result some of the skull elements of PETMG F.174 give longer measurements than comparable

elements in other specimens which have been calculated as larger and older. This is a reflection on the care that was taken to lift PETMG F.174, and the abrasion of the historical material subsequent to collection, resulting in the loss of many thin and fine bone extremities.

The degree of bone resorption in this animal has meant that its bones frequently act as cavities filled with clay that is often highly sulphurous. This can later develop pyrite rot while in museum collections, a condition that the bones of *Leedsichthys* are more vulnerable to damage from, because of their comparatively thin periosteum compared to the more robust marine reptile bones from the Oxford Clay. This is another reason why many historically collected specimens are more damaged and fragmentary today, than when first accessioned.

Smith Woodward's measurements were important in retrospectively identifying the specific elements that he used for his description, but of even greater importance was the system of marking specimens used by the BM(NH). Red markers were applied to those referred to in a description, and green markers applied to those specimens figured. Of more doubtful nature is the white markers, which appear on the two flat bones referred to by Hulke and Smith Woodward instead of the red markers used for the rest of Smith Woodward's described material. However, this does not explain the occurrence of a white marker on a BMNH P.6921 ceratohyal. Some bones that should be present with red markers (see section 8.3.1.7) appear to be missing, but may have become separated from the type material.

8.3 – OSTEOLOGICAL DESCRIPTIONS

Arthur Smith Woodward attempted to identify the bones present (1889b), but in the wake of the tentativeness of his own osteological identifications, he confessed to regarding all his identifications as unreliable beyond the gill rakers and the fin-rays (Leeds & Smith Woodward 1897). Since then, little has been done to critically assess these identifications, and although only a comparatively small number of specimens have been found over the ensuing years, it is worth reexamining his identifications, in the hope of further clarity as to the osteological nature of these elements. As such, his initial type material (which remains unfigured, save for two fragments of the eighty nine gill rakers present that were respectively illustrated in 1890) will be reexamined in conjunction with his descriptions, where necessary reidentified, and other skeletal elements identified wherever possible. As Schultze (1993) has observed, there are different approaches to the nomenclature of skull

roof elements, and for that reason it should be noted that here the approach advocated by Westoll (1943) will be followed (i.e. the parietal/post-parietal system, rather than the frontal/parietal). For each bone, Smith Woodward's description will first be repeated, followed by an assessment of the identification and reference to other related bones, with respect to the same elements being present in other specimens.

It should be noted that descriptions of aspects of the pectoral fin, caudal fin, gill raker and gill basket have already been made in chapters 5, 6 and 7.

8.3.1 - Descriptions of holotype bone morphologies of Smith Woodward

8.3.1.1 - "*A large flattened bone, of the kind already described by Mr. Hulke. It measures 2ft. (0.61m.) in length by 1ft. 3in. (0.38m.) in maximum breadth, is of a squamous character, thinning at each margin, and consists of two thin hard layers separated by a middle layer of soft diploë. In form and characters the bone is very suggestive of a* ***frontal*** *element.*" (Smith Woodward 1889b p.452)

Hulke (1887) referred to two bones in Alfred Leeds' collection as stegosaur dermal armour (fig. 8.2a-c, later noted by Seeley, CAMSM J.46874), and Smith Woodward referred to both of them as part of BMNH P.6921, the holotype of *Leedsichthys*. Of the two bones referred to by Hulke as stegosaurian armour, both have white markers to distinguish them, but Smith Woodward does not indicate which of the two he uses for his description. The dimensions of the bone in question are given by Smith Woodward as 61cm by 38cm, and despite extensive work to repair the material, the maximum dimensions of the bones do not now exceed 449mm by 311mm (fig. 8.3a) and 411mm by 288mm (fig. 8.3b). Hulke (1887) reports their dimensions as being 50cm and 80cm ("...the present breadth of one being not less than 50 centim., and that of another about 80 centim." Hulke 1887, p.702), which implies that by the time these bones reached Smith Woodward for description at the British Museum (Natural History), they had already become significantly damaged. It is likely, from the character of other fragments, that more can be reattached to these specimens to extend their current maximum dimensions, but further connections have not proved possible at this time. The bone with smaller dimensions strongly resembles the parietal of *Leedsichthys* as noted elsewhere (see Chapter 5) for the juvenile Cambridge specimen (CAMSM J.67420, length 211mm by 98mm wide, fig. 8.4) and 'Ariston' PETMG F.174 (a fused pair of length 555mm), both in terms of its radiating texture and the height of its central boss (increasing the centre of the bone's depth from 10mm to 18mm). The Cambridge parietal is almost complete, lacking only part of its medio-

posterior border, whereas the BMNH P.6921 parietal has no trace of the original perimeter of the bone. Its broken edges reveal a depth to the bone averaging 6mm, with a 1mm layer of clay in the centre, filling the void presumably created by resorption and remodelling. It is noteworthy that the juvenile parietal does not possess the gap filled with clay, a possible sign to indicate that the bone resorption and remodelling had not progressed to the extent of creating the internal cavity seen in the apparently larger individual represented by the holotype.

The larger of the two bones may be the left parietal, but again lacks any original perimeter with which to determine the outline of the bone. If it is a left parietal, it is hard to determine this through comparison with the Cambridge specimen, because the area near its original outline that is best preserved, is the area that is missing on the Cambridge specimen. Coupled with the noted problems of suture or perimeter variation of skull roof bones (Grande & Bemis 1998, Hanken & Hall 1993), it could be extremely difficult to determine this bone without further reconstruction. The superior surface of both bones is tan brown and smooth in the centre, with very light surface striations appearing outwards from this region. The inferior surface of both bones is again similar, a cream colour with a very fine fibrous surface texture with more deeply incised striations. The inferior surface of both bones has been cracked prior to fossilisation. The more pronounced radially striated character is repeated on the inferior surface of the Cambridge parietal.

Elements similar to it are reasonably commonplace in other specimens (GLAHM V3363 [fig. 8.5] has the 515mm highly fragmented remains of another right parietal, a 381mm left parietal [fig. 8.7] forms part of the LEICT G128.1900 and a right parietal 387mm long with some damage to its posterior edge constitutes part of BMNH P.11824 [fig. 8.6]), but the delicacy/fragility of the frequently-damaged bone perimeters means that the exact shape has been hard to define, and thus the bone hard to confidently identify. As an example, BMNH P.11823 may have a 412mm left parietal, or it may be another element of the dermatocranium, as its outline is ambiguous. Parietals have been recognised articulated with dermopterotics in PETMG F.174, but both bones await description after full preparation.

8.3.1.2 - "*An elongated bone, 1ft. 8in. (0.58m.) in length, somewhat broader at one extremity than at the other. One long margin is thickened and rounded, while the other is a thin edge; and the broader extremity is thicker than the narrower. This may perhaps be identified as the* ***angular***." (Smith Woodward 1889b p.452)

Of the bone marked with red paper that Smith Woodward originally described as a possible angular, only 511mm of its length can be restored (fig. 8.8a,b). At its maximum width, the bone measures 97mm. Surveying the other specimens of *Leedsichthys*, it can be seen that there are several incomplete elements that bear a resemblance to this bone. All have the character of the shape of an elongated triangle with one long side thickened (this is the only side that is usually preserved intact) and the other long side a thin fragile edge, with a smooth presumed external surface, and thin striations that form elevated ridges running much of the length of the presumed internal surface of the triangle. The posterior edge of the triangle is the shortest, and is irregular and fragile. These elements represent at least two different components of the skull, with the bone bearing the red sticker being the posterior two thirds of a left **cleithrum**, a left (782mm long) and a right (1,017mm long) being represented in BMNH P.10000 (fig. 8.9), and further right cleithra in CAMSM X.50112 (836mm long, fig. 8.12), PETMG F.174/10004 (1,047mm, fig. 8.11) and BMNH P.8609 (625mm long, fig. 8.13). 405mm of a left cleithrum is located at the tip of the left ceratobranchial I in BMNH P.10156 (fig. 8.15), and another likely left cleithrum is CAMSM J.67475 (418mm long, which appeared to have a black carbonaceous coating as a layer on its inner surface, with a 258mm fragment of a right CAMSM J.67474, fig. 8.14) which covers almost the same two thirds proportion of the bone as in BMNH P.6921, but the thin extended sheet of bone is almost entirely removed, leaving only the rounded anterior edge. The cleithrum can be distinguished from the other elements in having a thickened anterior edge that is fully rounded, curving smoothly back on to the internal surface. In more complete specimens, the tapered end of the triangle expands again into a shorter lower blade with the previously convex surface becoming concave. It is worth noting that Smith Woodward may well have later recognised that this bone was not an angular, as he notes the similarity "in miniature" in a specimen of *Saurostomus esocinus* to the 'supraclavicle' found in *Leedsichthys* (1916) despite not having explicitly described a 'supraclavicle' in 1889.

One of the other elements similar to this bone is the **maxilla** (left maxilla, 695mm long, GLAHM V3363, fig. 8.16a), which is distinguished by expanding slightly into a clearly fimbriated end after tapering, rather than expanding into a further blade. This matches the patterns observed in *Saurostomus* (SMNS St.52472, fig. 8.16b). Another difference between these two bones is the nature of the curve from the external to the internal surface, which is gradual in the cleithrum, but ends abruptly at its maximum medial point in the maxilla, changing into a flat perpendicular surface to the blade of the bone, forming a

ridge. This bone is only known in GLAHM V3363, although possible fragments exist within BMNH P.6925.

Another skeletal form that is similar to the cleithrum is represented by two mirror elements (BMNH P.6921 506mm long and BMNH P.6927 432mm long, both broken, fig. 8.17) that may be lower jaw components (angular or prearticular) but are too fragmentary to determine. They have a similar pattern of striations and rounding, but the element that is part of BMNH P.6921 has a very straight edge compared to the cleithrum of the same individual which has a broad curve with a slight angle midway along. Another similar component (513mm long) is found in GLAHM V3363 (fig. 8.17). It has a more complete tapered end, but variations in striation pattern on both surfaces, and the incompleteness of the flared and blade edges make a confirmed identification uncertain. This was previously considered to be a possible dentary, prior to the discovery of specimen BMNH P.66340.

Other fragments that look as though they are from similar elements to those above are present in BMNH P.6930.

8.3.1.3 - "*An elongated bone, 1ft. 3in. (0.38m.) in length, and the broader extremity of the corresponding element of the opposite side. This is probably the* ***hyomandibular****. The supposed upper extremity is somewhat expanded, and near this end on the posterior outer margin is a small facette, evidently for the operculum. For two-thirds of its width the bone is thick, but the anterior third is thin, as is also the inferior extremity.*" (Smith Woodward 1889 b p.452)

This element was the most difficult to identify amongst the remains of BMNH P.6921. A considerable amount of reconstruction was necessary before it could be identified, and even then only 368mm could be reconstructed (fig. 8.18), although judging by old glue traces near the tip there are likely to be further fragments that can be reattached. Apart from its fragmented condition, a significant reason for the difficulty in identifying it from Smith Woodward's description, is that it is not actually a hyomandibula, but a **hypobranchial** (Mainwaring 1978: fig.14). This can be determined by reference to the four hypobranchials contained within BMNH P.10156 (see Chapter 5), in particular the complete, fully prepared and uncrushed example (398mm long, fig. 8.19). The "small facette....for the operculum" referred to by Smith Woodward is actually the slightly crushed and distorted anterior articular surfaces of the hypobranchials. There are four hypobranchials amongst BMNH P.6921, but Smith Woodward only referred to two, as

supported by the red markers on the ones that are 368mm and 211mm in length (fig. 8.18). The other two examples in BMNH P.6921 are 235mm and 222mm long (fig. 8.18).

The hypobranchial frequently suffers from longitudinal crushing, presumably as a result of dorso-ventral weakening through internal bone resorption and remodelling. Its sub-oval anterior irregular articular surface gives way to an almost flat sheet of bone that extends to a square posterior end with a deeply striated dorsal surface and a ventral surface more smooth than striated (fig. 8.19). The anteriormost tip of the ventral surface is frequently broken and folded down on to the articular surface.

No more than five hypobranchials have been recovered for a single specimen. Specimen BMNH P.10156 indicates that there are at least six hypobranchials (three are partially preserved in position on the left side, with the single hypobranchial from the right prepared out in full). It would be expected that there would be eight, and it may simply be that not all of them have been recovered from historical digs. It is also possible that two hypobranchials (for the fourth branchial arch) might simply not have ossified during the life of the animal.

This element has probably been the most frequently misidentified, as Michelis *et al.* (1996) referred to it within the remains of the Wallücke *Leedsichthys* (WMfN PM 17006/8) as a tail-spine from a stegosaur (fig. 8.20a-c).

Other examples are in GLAHM V3363 (lengths: 283mm, 235mm, 132mm, 335mm, 234mm, fig. 8.21), BMNH P.11823 (lengths: 196mm, 153mm, 112mm, fig. 8.25), CAMSM X.50115 (170mm long, fig. 8.22), CAMSM X.50118 (147mm long, fig. 8.22), LEICT G418.1956.15.5 (177mm long, fig. 8.24), LEICT G418.1956.15.2 (173mm long, fig. 8.24; fig. 8.25), NMW 19.96.G8/33 (243mm long, fig. 8.23) and NMW 19.96.G8/34 (170mm long, fig. 8.23).

8.3.1.4 - "*Portions of four long narrow bones, the largest being 2 ft. 5in. (0.735 m.) in length, and not more than 3½ in. (0.09m.) in maximum width. Each bone is comparatively hard, irregularly 'Y'-shaped in transverse section, and seems most nearly paralleled by the ossifications of the* ***branchial arches*** *in Teleosteans.*" (Smith Woodward 1889 b p.452)

The branchial elements proved difficult to recognise, owing to post-depositional crushing, fragmentation, and a tendency for gill rakers to not be physically associated with them, and

led Liston (2004a) to erroneously identify them as jaw elements. This perception only changed when uncrushed versions from the Callovian of Normandie were encountered in a private collection (see Chapter 4), and the nature of the elements became clear.

Although many specimens feature occasional branchial elements, there are two principal specimens that are responsible for guiding the identification of components of *Leedsichthys* gill basket structure. The first of these is BMNH P.10156 (see Chapter 5), which preserves all four ventral arch components in articulation and almost entirely intact (half the hypobranchials and some of the extremities of the eight ceratobranchials are missing). Although this reveals much about the layout of the ventral arches and their relative lengths (there is a 20% variation in length between the third and first ceratobranchials, from 810mm-990mm), they are relatively unprepared and therefore reveal little about the three dimensional form despite being unusually free from crush damage.

The second particularly informative specimen is the sub-adult BMNH P.11823 (see Chapter 7), which features a variety of nine (excluding the three hypobranchials) more or less complete branchial elements. Owing to its relative youth at point of death compared with most specimens, it has not experienced extensive internal resorption and remodelling, and so these elements have not been crushed flat (which produced Smith Woodward's noted description of "irregularly 'Y'-shaped in transverse section") as in the older specimens. This suite of fully prepared elements shows a diversity of form and length that, while bearing possible ontogenetic allometric change in mind and comparing with illustrations for other holosteans (Grande & Bemis 1991, 1998) suggests that there are six ceratobranchials (CBI: 481mm; CBII/IV: 458mm, 522mm, 474mm, 495mm; CBIII: 611mm) and three epibranchials (EBI: 394mm, 367mm; EBII: 269mm) present (fig. 8.26-8.28). The epibranchials are smaller than the ceratobranchials (the longest epibranchial, the first, is around half the length of the third ceratobranchial), with a branchial groove that crosses the outline of the rest of the branchial element, as opposed to staying within the outline and preserving a more or less triangular cross-section. The first epibranchial in particular is distinguished by an abrupt expansion in the last 20% of the medial side of the anterior end, which is not mirrored on the lateral side. Both first epibranchials are present in BMNH P.11823 and BMNH P.10000 (605mm, 542mm in fig. 8.29; other ceratobranchial fragments 497mm, 322mm, 318mm in fig. 8.30). Beyond these epibranchial diagnoses, it is suggested that the other epibranchial present in BMNH P.11823 is epibranchial II, owing to its relatively large size.

None of the holotype (BMNH P.6921) branchial elements reaches the 735mm length noted in the 1889 description (fig. 8.31), but judging from relative size, the four branchial elements that Smith Woodward referred to in his initial diagnosis of the taxon were two first ceratobranchials (680mm and 630mm) and two second epibranchials (475mm and 323mm). As with other elements, it is likely that some of the remaining unattached similarly-textured fragments will ultimately extend the current lengths of some of these bones further. As an example of this potential, a further epibranchial (357mm long) has been reconstructed from the fragments in the holotype material, meaning that there is one more branchial element than noted in the original 1889 description.

The lineations on the branchial elements of smaller (and presumably younger) individuals grade into a striated form creating a rugose texture in the largest individuals.

Other examples of branchial elements are in GLAHM V3363 (ceratobranchial ?III lengths: 760mm, 690mm, ceratobranchial ?I length: 583mm; epibranchial ?II lengths: 358mm, 381mm), PETMG F174 (ceratobranchial III lengths: 849mm, 756mm), BMNH P.6923 (661mm, 631mm), BMNH P.6926 (615mm, 452mm), BMNH P.6928 (514mm), BMNH P.6930 (477mm), NMW 19.96.G8/2 (299mm), NMW 19.96.G8/3 (352mm), NMW 19.96.G8/59 (530mm) and fragments in CAMSM J.67476, CAMSM J.67477, CAMSM J.67479, CAMSM X.50119, CAMSM X.50121, CAMSM X.50124.

8.3.1.5 – "*A very large number of small, narrow, elongated bones of peculiar shape, probably to be regarded as* ***gill-rakers****. The largest of these are about 3in. (0.075m.) in length, and 1/3in. (0.010m.) in width. Each is laterally compressed, slightly expanded at one extremity, and rarely straight, but irregularly bent or contorted. The surface is coarsely rugose, and one long border is rounded, while the other is cleft by a longitudinal median furrow. The rounded border is comparatively smooth, but the furrowed edge is coarsely serrated, a series of short oblique ridges terminating in points on each side.*" (Smith Woodward 1889 b p.452-453)

Smith Woodward's identification was indeed correct, as he later reinforced by regarding the gill rakers and the fin-rays as the only two elements of *Leedsichthys* skeleton which he was confident of the identification of (Leeds & Smith Woodward 1897). The detailed structure of this bone, and its diversity, has been dealt with elsewhere (see Chapter 6). It is hoped that a more thorough treatment of the variation of morphology of the gill raker

throughout the gill basket, and its palaeoecological implications, will be possible once all of PETMG F.174 has been retrieved, prepared and studied.

8.3.1.6 - "*Portion of a large squamous bone, longer (deeper) than broad, with one long margin thickened, rounded, and concavely arched. A nearly complete example of the same element, doubtfully forming part of the series, measures 2 ft. 9in. (0.838m.) in length, and suggests that it may be identified either with the* ***preoperculum*** *or* ***clavicle.***"(Smith Woodward 1889 b p.453)

It is hard to identify the first element that Smith Woodward refers to in this section. It may have become damaged following this description, resulting in the loss of the 'squamous' component that he refers to, as the only pieces within BMNH P.6921 today that bear any similarity to the bone described, consist merely of fragments of ridges.

The more or less complete second element that Smith Woodward refers to, is, however, more easily identified, as 810 of its 838mm length still remains, with its red paper marker and separate catalogue number of BMNH P.6922 (fig. 8.32). Again, the bone is vaguely triangular in overall appearance, with a slight curve forwards on its rounded edge near the pointed tip. A thin but extensive sheet of bone runs from the posterior edge of the ridge, bearing striations which may be related to annular growth (see Frost & Kipling 1959), but not enough of this feature survives in any specimen to further examine this. The concave ridge loses its antero-posterior curve and becomes straight around 40% down its length from the anterior tip, with the ridges becoming increasingly incised until they verge on elevated tubes or laminae, the more superior the position on the ridge. This does indeed appear to be the right preopercle, as Smith Woodward suggested, but there are bones of very similar appearance with distinctive characters throughout the hypodigm of *Leedsichthys*, that urge caution in identification of this form of bone in this animal's skeleton. A very similar bone has been identified as a left preopercle in PETMG F.174 (PETMG F.174/182, 572mm long; fig. 8.33), with a slightly more blunt and flat anterior tip.

Two bones from BMNH P.10000 (fig. 8.35) exemplify the variability in similar bones to BMNH P.6922. The first (659mm long) is very similar to BMNH P.6922, with a small sheet of thin bone extending on the anterior of the tip of the ridge. The second bone (691mm) has far less of a ridge, with the anterior edge forming more of a rounded thickening, with no real demarcation between the ridge and the sheet of thin bone, and a

flat sub-triangular articular facet replacing the tip at the anterior end. This second bone strongly resembles a 'butterfly'-shaped bone in GLAHM V3363 (fig. 8.36), so described because there is an angle of 140 degrees subtended by the junction of these two bones. The fusion in this specimen would be consistent with it being an older individual than BMNH P.10000, as suggested elsewhere (see Chapter 7). The first element (626mm long) is very similar to the 691mm element in BMNH P.10000, with part of a second element (145mm long) meeting it at the articular surface. The similar size of the two elements in BMNH P.10000 would suggest that they might be part of a series of bones with the preopercle. Alternatively, they might prove to be a fused plate of branchiostegals, although the 140° fused character in GLAHM V3363 would be difficult to explain within that scenario, unless that is purely a pathological condition.

Other examples are – Left preopercle (possible): GLAHM V3363 (772mm, fig. 8.34; see also Appendix VII/Liston 2006 figures 9 and 10); CAMSM J.66938 (593mm).
Left preopercular ridges; GLAHM V3363 (305mm); NMW 19.96.G8/30 (194mm); BMNH P.6925 (320mm); CAMSM X.50109 (714mm); BMNH P.10156 (820mm); LEICT G128.1900 (277mm).
Right ridges: CAMSM X.50113 (301mm); LEICT G128.1900 (145mm).

8.3.1.7 - "*Portions of eleven very dense, large, rib-shaped bones, only superficially ossified at the broader extremity, but terminating in a well-formed point at the distal end. These bones are rounded or irregularly quadrangular in section, are more or less arched, and vary considerably in relative width or thickness. The broadest and stoutest specimen is much arched, 1ft. 5in. (0.43m) in length; and a nearly perfect detached example of the same bone shows that this wants a length of at least 8in (0.23m) at the pointed extremity. The largest bone measures 2ft. 4in. (0.712m) in length, and is straightened; while the smaller examples are more curved and more rounded in section. These bones were evidently arranged in not less than six pairs, and Mr' Leeds' suggestion seems most plausible, that they are the* ***branchiostegal rays*** *of the fish.*" (Smith Woodward 1889b p.453)

Identification of these eleven bones amongst the remains of BMNH P.6921 is made slightly complicated by there only being nine with red markers visible (fig. 8.37), and there are a further four fragments of the same form of bone that are unmarked. The "broadest and stoutest specimen" is 458mm long, and the "nearly perfect detached example of the same bone" is probably the elongate curved element that has a red marker in BMNH

P.6925. The largest of the red markered bones in BMNH P.6921 can only be reconstructed to 612mm in length, and the other marked bones are only partially complete varying in length from 251-431mm (251mm, 263mm, 312mm, 339mm, 363mm, 427mm, 431mm).

The individual elements are elongate bones with a surface showing a 'woven' texture near the base changing into a more striated character towards the tip. They exhibit a varying degree of curvature, with the longest elements often the straightest and the shortest often the most extremely curved. The interior of the base is hollow due to bone resorption, and invariably is crushed inwards. This means that the transverse cross-section of the bone varies from an almost figure eight torus at this level, to a quadrilateral, then a subrectangular character, to circular, to a crenulated circle at the apex. Sometimes, the apex is transversely flattened, which produces a more elongate ovoid cross-section at this level. The bones have a posterior surface that sometimes exhibits signs of grooving for the adjacent element to fit in, and have a fundamental asymmetry, which means that they can be identified as lefts and rights. The ridged tip might be embedded in the body wall or be a structural support for connective tissue at the tip of a fin.

Also worthy of note is a retrieved accumulation of bones of this general morphology, forming a fragmented 821mm long block (fig. 8.10a), in which the clay matrix has not been fully removed from the bones, so that the clay supports the original relationships of the bones in the bed. Unfortunately, the bones have received extensive consolidation in the past with plaster, the moisture of which appears to have triggered pyritic decay of the bone, resulting in later chemical treatment of the fossil material in an attempt to halt this. Possibly as a result of this treatment, the clay matrix has begun to shrink away from the bones. Consequently both bones and matrix are highly unstable and fragile. However, one of the bony elements within this unit is a complete element of the form that Smith Woodward described, along with another (612mm) from the group of nine with red markers (fig. 8.37). It is of interest that some, but not all, of the bones in this block show an origin from a common point of divergence in a wide basal form. The possible meaning and function of this bifurcated origin will be dealt with later. None of these elements bear a specimen number, and reassembling the fragments into their original disposition reveals a pattern strikingly similar to that drawn by Alfred Leeds in a letter to Smith Woodward as a recent find (fig. 8.10b, Leeds 1894) long after the type material had been sent to London, and more than a year after it was accessioned at the BM (NH) in 1893. This raises doubts as to whether this group of elements actually belongs to the type material, or has simply

later been erroneously placed with BMNH P.6921, perhaps as part of the chaos ensuing from the January 1972 flatbed trolley incident.

Smith Woodward's communication of Alfred Leeds' interpretation of the 'rib-shaped' elements as branchiostegals was modified by himself in 1895, saying that they would "most likely prove to be vertebral arches". Smith Woodward's later identifications in a specimen of *Saurostomus esocinus* made reference to bones "in miniature" identifiable in *Leedsichthys*, particularly commenting on the "neural arches fused with their curved spines" which are likely to be referring to the same elements (1916). This suggests that he had found little reason to doubt his identification of this element since 1895.

In the meantime, the collector Henry Keeping had furnished the Woodwardian (now Sedgwick) Museum of Cambridge University with a set of these bones, linked in places again with intervening clay matrix which appeared to preserve a sense of the *in vivo* relationship of these elements. Noting that Hoffstetter (1957) had dismissed von Huene's (1901) interpretation of these elements as stegosaur tail spines (which von Huene figured with a stegosaur armour plate to underline his argument, see fig. 2.3), Liston (2004a) observed that if these bones were ribs then the curvature observed would imply an animal whose rib cage expanded and contracted extremely quickly over a very short distance, in a similar way to the sunfish (*Mola mola*). Dismissing non-elongate meristic elements (Nursall 1956, Jarman 1961), Liston suggested that these bones more resembled the fin-rays found in the dorsal fin of *Saurostomus* (2004a), a conclusion later discovered to have been reached independently by Alfred Leeds in 1898 (Liston & Noè 2004). This would be consistent with the numbers of this specific form of bone found in various specimens ranging between half a dozen and a dozen, rather than a number reflecting many vertebral segments of a meristic element that repeats throughout the axial skeleton. It should, however, also be noted that restricted ossification of ribs has been observed in a series of pachycormids to a variety of degrees (see 7.2.1), which might account for an unexpectedly low number of ribs preserving in *Leedsichthys* as well.

To return to Smith Woodward's original diagnosis, McAllister (1968) found that the diagnostic form of branchiostegals in pachycormids was a thin blade-like element ('filiform'), and that there were usually between thirty and fifty of them. These long thin elements, resembling elongate varyingly curved cones, are very far removed from this description, and do not present the articulation between adjacent distal tips that would be expected. It might indeed be that the bones mentioned above as possible fused

branchiostegals forming a single plate are the correct identification of the branchiostegal in *Leedsichthys*, although equally the branchiostegal rays might simply have been another bone in this animal's skeleton that did not ossify.

Once the branchiostegals have been eliminated as candidates, then as elongate meristic elements these bones can only be either directly related to the vertebra (supraneural, haemal spine, left or right pleural rib) or to the fins (e.g. Wenz 1967: fig.62). Specimens that preserve part or all of the pectoral fin (PETMG F.174, BMNH P.10000) and caudal fin (BMNH P.10000) allow these appendages to be ruled out of consideration with regard to these bones, which leaves the median fins: dorsal, anal, pelvic. In Pachycormidae, the pelvic fin is only recorded in the genus *Orthocormus* and no diagnostic pelvic element has been recorded for *Leedsichthys*, but the anal fin appears to be present in virtually all taxa (including *Asthenocormus* and Taxon 13). The dorsal fin is ubiquitous throughout the group. The anal fin would not be expected to display left/right asymmetric elements.

In terms of elements related to vertebrae, the same reasoning for the elements figured by von Huene not being ribs (i.e. the speed of increase and reduction in size) also applies to them as vertebral arches/supraneurals. In addition, the curvature of the bones (upwards and back) is counter to the curvature seen in the supraneurals figured by Wenz (1967) and Bartsch (1988) (backwards and up). The left/right asymmetry would be consistent not only with pleural ribs, but also with the left and right layers of hemitrichia in the dorsal fin that can be seen in some pachycormid specimens (e.g. *Asthenocormus* JM SOS 542 and JM SOS 3556; fig. 8.40c,d). It would not be expected for the haemal spine, as a median structure, to display such asymmetry.

The occasional branching character of these bones is extremely unusual, presenting in one or two of the bones figured by von Huene (1901), in the 821mm block in the holotype (BMNH P.6921, fig. 8.10a), GLAHM V3363 (617mm long specimen, fig. 8.39a, fig. 8.39b) and BMNH P.11826 (545mm long; fig. 8.39b). Leeds himself remarked on it in a letter to Smith Woodward in 1894 with a sketch of the as yet unlocated (if it is not actually that depicted in fig. 8.10a) specimen, querying what Smith Woodward thought that the bone might be (Leeds 1894). Smith Woodward's reply is unfortunately not recorded. The specimen cannot be traced to any collection in the UK, and may have been later sold via the Bonn dealer Bernhard Stürtz to one of the many museums in mainland Europe that hold material collected by Alfred Leeds (Liston 2004a, see Appendix VII/Liston 2006). The bifurcation, which could also be the result of a fusion of adjacent elements, varies in

dividing into two (GLAHM V3363, SMC J.46873), three (BMNH P.11826) and four (as drawn in the letter from Leeds in 1894) branches. What is even more remarkable, is that in a further specimen this antero-posterior fusion or bifurcation is paralleled by a lateral bifurcation in the same element. The specimen, recovered from an Oxford Clay brick pit remains in private hands, but a cast has been retained in the collections of the Hunterian Museum (GLAHM 109441; fig. 8.40a,b). It seems unlikely that this specimen would be part of a fin element unless it was entirely within the body cavity as a supporting element between the vertebral column and the external fin. However, it is worth noting that it is likely that fusion of occasional elements in the vertebral column would help confer rigidity on the axial skeleton, and so enhance locomotive efficiency. This raises the possibility that these are in fact supraneurals, but (as noted in the preceding paragraph) growing with a curvature counter to that experienced in other pachycormids (Lambers 1992).

8.3.1.7.1 - Curvature Analysis: It may be that these elements, with their variety in curvature of otherwise morphologically conservative bones, might represent a convergence of structure of disparate meristic components. The shape and architecture of a bone reflects the stresses that it operates and grows within (Hanken & Hall 1993) and the mechanical environment around it (Thomason 1995). If the degree of curvature reflects the improved predictability for dynamic loading and loading direction (Bertram & Biewener 1988), then it might well be possible to distinguish between (for example) the mechanical environment of a dorsal fin support and that of a haemal spine. Demonstrating that equal stresses and strains occurred in corresponding points of different animals moving in similar gaits (Biewener & Taylor 1986), Biewener also demonstrated that the shape and mass of a bone appeared to represent selection of adaptive remodelling to its unique mechanical environment (1983a). This also related the mass of the animal to the degree of curvature of a specific bone. Following his work, two assessments were made. The orthogonal distance (X, the moment arm of the axial component of force acting on a bone) was measured from the chord (2L) between the proximal and distal ends (fig. 8.41a) of a series of four bones (fig. 8.41b) that appeared unique to the skeleton of *Leedsichthys*. These measurements were then applied to the equation:

$$\xi = X/2L \times 100$$

The normalised bone curvature (ξ) was then used as a measure of relative mass of the *Leedsichthys* specimens concerned. A ranking of specimens was then produced. The bone in question is unusually robust and preserves well with little internal resorption, is believed

to only occur at one meristic level within the animal (possibly as a left and a right rather than simply as a medial element) and thus was selected as a good index bone for comparison between specimens.

Secondly, the normalised bone curvature for a series of thirty elements from GLAHM V3363 was calculated and plotted against bone length. It would be predicted that a series of meristic elements from a single individual, if representing a variety of different elements, should characteristically plot in discrete groups, with discontinuities between stress regimes. This then might aid in describing the bone types in terms of different locations in the animal's body. GLAHM V3363 was selected for this purpose, as it has an unusual diversity of form representing the full range of forms of these elongate bones, which have traditionally simply been referred to as 'rib-shaped bones'.

8.3.1.7.2 - Curvature Results: From curvature results, assuming that the principle of declining curvature with increasing mass holds true (Biewener 1983b), the rank order of the specimens, from largest mass to smallest mass, is NMW 19.96.G9/2, BMNH P.11825, GLAHM V3363, BMNH P.6925.

When the data for the series of elements from GLAHM V3363 was plotted (Appendix V), three distinct bands of curvature emerged. The elements within those bands were compared to ascertain differences and similarities, to erect groups and suggest locations for the bones within the skeleton of *Leedsichthys*.

Band 1 (curvature range 0.28-5.71): Low curvature with short lengths, possibly anal fin elements (2 and 3). Moderate length with (10, 11) and without (14, 1) thick lateral flanges of bone. Longer elements show a thin ridge which resembles a feature for anchoring intercostal muscles, therefore may represent pleural ribs (16, 26, 4, 23, 28). Exceptionally straight and long elements (29, 22, 27) seem to also be ribs, presumably anterior elements, although 27 lacks a clear attachment ridge for muscle.

Band 2 (curvature range 9.57-14.64): Moderate curvature with moderate length (21, 25) also seem to be ribs with a ridge for presumed intercostal muscle attachments. Other elements that lack this feature (7, 8, 9, 12, 13, 15, 17, 24) resemble dorsal fin supports, as in CAMSM J.46873. The identity of the shorter elements in this curvature band (5, 6) is unclear.

The sole element in the gap between the moderate and high curvature regions is a bone with a distinctive curvature, similar to a supraneural (18) (Smith Woodward 1916).

Band 3 (curvature range 19.44-24.14): The high curvature range has three elements within it, two of them being the robust elements used for the mass comparison (19,31), and the third element a similar size of bone but with a more cylindrical than tear-drop-shaped cross-section (30). The location of these elements is unclear: they appear too long to be bearing the stress of locomotion at the caudal end of the body, so presumably are an anterior feature, at the front of the postcranial part of the skeleton. They also bear grooves in the posterior surface, for adjacent bones to sit within.

8.3.1.8 - "*The **fin-rays** are most remarkable, and, judging from the position in which they were discovered, the known specimens may all probably be assigned to the pectoral fin. They consist of fibrous bone, and appear as if composed of numerous long, tapering bony splints, incompletely fused together. The two halves of each ray remain separate, and in some cases they have been proved to attain a length of not less than 5ft. (1.525m.). There are no transverse joints, but all the rays exhibit numerous bifurcations, and Mr. Leeds estimates that the distal extremity of each of the largest becomes divided into at least thirty-two small branches.*

"*Smaller more slender fin-rays, probably of the same type of fish, have also been discovered in the Oxford Clay of the same locality. These are gently rounded and transversely articulated, thus suggesting that the specimens just noticed are characteristic only of a powerful pectoral.*" (Smith Woodward 1889 b p.453)

Comparing the fragments of fin-ray present in BMNH P.6921, with pieces observed during the excavation of two pectoral fins during the Star Pit dig in the summer of 2002 (see Appendix VII/Liston 2006), it does appear that they are part of the pectoral fin. From the fragments remaining today, however, the maximum length of ray that can be reconstructed is 697mm (fig. 8.42a), rather than the 1.5 metres stated by Smith Woodward. Although the recorded length of the pectoral fins recovered from the Star Pit reaches a maximum of 1363mm, it should be remembered that the pectoral fins have not been fully prepared from their plaster jacket and that estimates of the age and length of BMNH P.6921 are significantly greater than for PETMG F.174 (see Chapter 7), therefore it would be expected that the pectorals (being the lifting surface for the animal) would be larger with more extensive rays in specimen BMNH P.6921.

Aspects of both pectoral and caudal fins have been described elsewhere (see Chapter 7). Once the pectoral fins from PETMG F.174 have been prepared, it is hoped that a fuller understanding can be gained for the way in which the rays vary from proximal to distal ends, so that the distinction between ray fragments from the caudal and pectoral fins can be more clearly defined. The rays are similar in bifurcating without segmentation in both types of fin, with the rays being sub-circular in both at some points. Once the details of the transformation of the pectoral fin-ray as it extends from body to tip become clearer, more precise distinctions should be possible, and as such the following distinctions may be premature to present. Suffice to say that for BMNH P.6921 no red markers have been found on ray fragments to indicate that they were specifically used during the writing of the 1889 description, and there appear to be both pectoral and caudal fin-ray fragments present. A significant amount of reconstruction of the fin-rays has been done, but the longest fragment reaches only 697mm, very short of the 1520mm Smith Woodward suggests as the maximum length determinable (although he is vague about how this figure has been arrived at, which suggests some extrapolation has been made, rather than a simple measurement of a single continuous element). The most complete isolated **caudal fin-ray** element known is the 1225mm long GLAHM V3362 (fig. 8.42b). The structure of this ray is typical of the fragments in BMNH P.6921 and others, and will be used to describe the morphology of this type of ray.

The proximal end begins as a roughly triangular plate (57mm wide) made up of fused overlying sheets, that tapers over 144mm to a 25mm wide 'neck'. At this point, the ray is in the form of a 'V'-shape, with the posterior edge being the groove of the 'V'. This form holds for 115mm, until the first bifurcation. At this point, the posterior ray has a grooved posterior surface and a convexly curved anterior surface, giving the ray a crescent-like cross-section. The anterior ray, in contrast, has the cross-section of a right-angled isoscelean triangle, with two to three reinforcing ridges running down the 'hypotenuse' surface of the triangle. The posterior ray loses its curved posterior surface after 150mm, replaced by a similar 'ridged-hypotenuse' surface and right-angled isoscelean triangle in cross-section, just like the anterior ray. It gradually changes over the ensuing 250mm into a subcircular cross-section ray, and 300mm later bifurcates, both of these rays tapering to termination 165mm later. The anterior ray retains its isoscelean cross-section for 430mm before it bifurcates into two subcircular rays, the anterior branch bifurcating again 275mm later (both terminating within 105mm) and the posterior branch terminating without further bifurcation 430mm further on.

In contrast, the **pectoral fin-ray**, as has been noted previously (see Chapter 7) has a flatter character, more 'U'-shaped in cross-section, with the tips of the 'U' sharp, tending towards elevated laminae above the main body of the ray. The surface of the ray is frequently pock-marked by scattered recesses. After some repair work, the most complete extent of one of these pectoral fin elements in BMNH P.6921 is 568mm long (fig. 8.42a), and it will be described as representative of other pectoral elements, pending further preparation of the pectoral fins of PETMG F.174. The ray is 19mm wide at its slightly damaged proximal end, with ridging along its proximal anterior surface, and a smooth posterior surface as it expands to its maximum width of 29mm. After 69mm, the ridges have coalesced into both laminar edges of the 'U-'shaped ray described above. This ray continues for 240mm, tapering to a 19mm wide ray before bifurcating, a ridge developing in the centre of the groove between the two laminae that splits into the posterior and anterior laminae of the anterior and posterior branches respectively. Both branches continue 260mm (posterior) and 265mm (anterior), where the broken ends have tapered to 12mm high.

As noted earlier, this does suggest that there is a distinctive character to caudal and pectoral rays to help in their identification, but bearing in mind that the BMNH P.10000 pectoral fin fragment indicates some changes in character across as well as along the pectoral fin, a more complete understanding of the character of these rays awaits the full preparation of these pectoral fins. In the meantime, it is worth noting one other element from the pectoral fin, believed to be the distal **actinotrichia** (Videler 1993) (fig. 8.42c). The distal elements of these bones were seen at the very tips of the pectoral fins in the very early stages of the excavation of PETMG F.174 in July 2002 (see Appendix VII/Liston 2006), and identification of them within other specimens of *Leedsichthys* (e.g. BMNH P.6921) shows that they are discrete elements, with no preserved contact to other bony structures, tapering to terminations at both ends. There are at least five examples of this bone in BMNH P.6921, the most complete of which (bottom of fig. 8.42c) will be described here.

501mm long, this element is broken at the mid-point into two halves. The proximal part (at the left of fig. 8.42c) resembles the thick ribbed ridges of the pectoral and caudal elements just described, but it is divided into two unequal lengths with a 'V'-shaped horizontal gap between them. Around halfway down the length of the longer element the gap is filled between these circa 13mm wide branches by a thin plate sheet. Two thirds along the thin bony plate, a vertical ridge rises on the dorsal surface and joins with the two

proximal rays. This forms a 'λ'-shape in transverse cross-section, with the ridge forming the angled 'leg' of the lambda, and the two elements that arose proximally forming the two halves of the long straight line of the Greek letter's form. From this point (215mm from the proximal tip), this three-branched structure continues for another 75mm, at which point the shorter anterior element turns posteriorly by ten degrees, the posterior element turns posteriorly by around seventeen degrees, and the ridge bifurcates to provide a 2mm wide attenuated prong to each 6mm wide ray. The bifurcation is also marked by the presence of a vertical semicircular ridge that emerges on the posterior surface of the thin bony plate. Each attenuated ray continues to taper to termination over around 200mm, with a flat ventral surface and a convex dorsal surface made up of the attenuated prong.

These distal terminations were found at the tips of the pectoral fins of PETMG F.174, prior to the fins being lifted from the clay. More detail about the structure of the pectoral fins is expected to emerge as the material from this dig continues to be prepared from its clay, glue and plaster jackets, which will also enable their close comparison with the 900mm long apparently pachycormid paired pectoral fins from the Solnhofen lithographic limestone (Tithonian) on display in the Bayerische Staatssammlung für Paläontologie und Historische Geologie, München (BSPG 1951.xvi.1). Two elements from PETMG F.174 have already been identified as **radiales** from the right fin (fig. 8.43: radiale I, PETMG F.174/245 199mm x 79mm and radiale II, PETMG F.174/263 250mm x 92mm) from material prepared so far, enabling identification of more fragmentary remains of these elements in other specimens (e.g. fig. 8.44: BMNH P.6921 has a 118mm long radiale II fragment and a 101mm long radiale I fragment). Both elements feature the characteristic flaring thin bone at the distal end of a long tapering triangular strut of bone. On each surface the anterior and posterior walls fold round at the neck to nearly touch, forming a groove. The expanded area of thin bone does not fully ossify, leaving a hole in the middle of the triangular bony sheet. This compares well with fins of other pachycormids figured by Jessen (1972).

Other examples are in GLAHM V3363, BMNH P.6929.

8.3.2 - Descriptions of further bone morphologies

8.3.2.1 - Cranial:

It is worth noting that since Smith Woodward's misidentification of the hypobranchial of BMNH P.6921 as a hyomandibula, true **hyomandibulae** have been recovered for *Leedsichthys*. The most striking is the left hyomandibula preserved as part of the gill

basket specimen BMNH P.10156 (fig. 8.45a,b). 687mm long and 435mm wide across its expanded frill (292mm wide across its upper edge), the fossa on its internal surface is clearly visible. Its external surface is flat, and its internal surface convexly curved (Wenz 1967: fig.59). This hyomandibula is unusually well-preserved in three dimensions, as with most of specimen BMNH P.10156, due to its preservation in a concretion. It was erroneously figured (Martill 1988, Fig.1b) as a ceratohyal. Both hyomandibulae have been recovered for PETMG F.174 and await preparation, but one was recorded as 663mm in length prior to recovery. A pair of hyomandibulae also occurs in the sub-adult specimen BMNH P.11823 (a left of 557mm and a right of 487mm; fig. 8.46a,b). A badly damaged left hyomandibula has been measured at 650mm in length from BMNH P.10000. Also, a heavily pyritised 505 x 260mm partial right hyomandibula (CAMSM J.46873a, fig.8.49) forms part of the specimen that von Huene figured as a stegosaur (1901).

In relation to the hyomandibula, a possible 390mm long **symplectic** has been noted by Martill (pers. comm.) within a concretionary slab of Oxford Clay (LEICT G128.1900; fig. 8.51a,b), but its outlines are difficult to be certain of, and only preparation of the bone out of its surrounding clay (and a 596mm ceratobranchial) could confirm or deny this identification.

The **ceratohyal** (see Lehmann 1949: fig.17) is probably the most robust cranial element of *Leedsichthys*, and as such is moderately common within specimens. It is present in BMNH P.6921 (fig. 8.52), and will be described from that specimen.

The left ceratohyal is 290mm long but broken at both anterior and posterior ends, with sections missing from its inferior border. It has a maximum (posterior) width of 149mm, tapering to a minimum (anterior) width of around 118mm. It is highly rugose on both surfaces, with the internal surface flat and the outer surface convexly curved at its superior edge, and a radiating pattern of striations emanating from the middle of this superior ridge. This means that the bone thickens in cross-section from its blade-like inferior edge up to its superior edge, creating a thickened ridge or bar that gives the bone a 'teardrop' appearance in transverse section. There are other ceratohyals, of vertical width 100mm (PETMG F.174, still in plaster), 125mm (BMNH P.10000) and 141mm (GLAHM V3363, fig. 8.53), but the only specimen that possesses any part of its posterior or anterior edge is the exceptionally fragile and pyritic BMNH P.10000 (fig. 8.50). The left ceratohyal here displays a border with an anterior extension of the lower half of the bone, into a thin longitudinally-curved sheet of bone.

The smallest ceratohyal known is 66mm wide, from the subadult specimen BMNH P.11823 (fig. 8.54), although it also bears a strong resemblance to the metapterygoid as depicted by Lehmann (Lehmann 1949: fig. 5). The largest ceratohyal known is most probably represented by fragments above the clay overlying the distal ends of the left first three hypobranchials of BMNH P.10156, but its width cannot be reconstructed with confidence. This specimen also features a pair of **hypohyals** (see Lehmann 1949: fig. 17) (fig. 8.55a,b), the left (170mm long) still embedded in clay at the base of the left hypobranchials (BMNH P.10156/7), and the right (168mm long) prepared entirely out of the clay (BMNH P.10156/1). The dorsal surface of the right hypohyal is highly ridged anteriorly, with a smooth ventral surface. A characteristic medial indentation gives rise to a shelf that runs antero-ventrally along part of the medial edge. A further left hypohyal, 132mm in length, occurs as part of BMNH P.66340 (fig. 8.56).

Other examples of ceratohyals are in BMNH P.6928 (a left, 439mm long; fig. 8.58), BMNH P.47412 (a left, 591mm long; fig. 8.57), and CAMSM X.50114 (a right, 402mm long; fig. 8.59).

A far more rare cranial element is the **parasphenoid** (see Lehmann 1949: fig. 4), known only from two specimens, BMNH P.10000 (fig. 8.60) and LEICT G1.2005 (fig. 8.61a,b). In dorsal view, the 404mm long Leicester specimen shows advanced central fusion of both left and right wings of the parasphenoid, extending from the level of the notch for the internal carotid artery, posterior to the aortic notch, whereas the larger (598mm long) BMNH P.10000 element shows, somewhat surprisingly, no fusion at all between the two wings over this distance. Instead, BMNH P.10000 preserves a distinct vertical ridge at the medial edge of each wing. Both specimens show a common convex camber to the bone in dorsal aspect, interpreted as marking the floor of the ventral compartment of the myodome (Patterson 1975: fig. 141 and 142). Ventrally, the bone is flat and smooth in BMNH P.10000, but curved in LEICT G1.2005. As the bone extends posteriorly it changes from a continuous unit to a series of individual rays. Anteriorly, by the junction of the two wings, the bone becomes thicker and flatter in both specimens, with a broken perimeter obscuring its true anterior extent and form.

Above the parasphenoid sits the **basiocciput** (Rayner 1948: fig. 16; Grande & Bemis 1998), extending from the junction of the wings of the parasphenoid posteriorly to the occiput. Only two specimens preserve this bone, GLAHM V3363 (fig. 8.62a,b) and

LEICT G128.1900 (fig. 8.62c,d). The dorsal surface of both specimens is extremely rough, suggesting a cartilaginous covering might have been present in life. In death, both bones have filled with bivalve shells (and a fragment of an unidentified further cranial bone) in thick clay like a large semicircular cross-section drainage gutter. The description of this bone will be primarily based on the better preserved GLAHM V3363 element. On the ventral surface of this bone, a prominent ridge runs down the centre for three quarters of its length from within a smooth diamond-shaped facet (that could be the aortal facet) anteriorly to where the convex surface starts to change into a bilobate form (in transverse section like the shape of a number '3' rotated through ninety degrees). As the bone curves from this ridge to its dorso-lateral extent, it becomes highly rugose, and having reached an angle of around 45 degrees to the horizontal, it changes to a flatter angle of only ten degrees from the horizontal. The only true trace of the original edge of this bone appears to be the thin postero-lateral edge on the right of this specimen. In contrast with GLAHM V3363, in LEICM G128.1900 a substantial part of the ventral surface is obscured by an indeterminate fragment of bone (although an elongate prong emerging from one edge makes the fragment reminiscent of a **prootic**). The central ridge and radiating rugose texture is still visible in this specimen. The ventral foramen is not visible in either specimen, and this is presumed to be due to the degree of damage at the posterior end of both elements.

The **dentary** (see Lehmann 1949: fig.2) is only known from one specimen of *Leedsichthys*, BMNH P.66340 (fig. 8.63a-c). This bone was previously misidentified as the premaxilla of the ichthyosaur *Ophthalmosaurus* (Neaverson 1935:p.239). It is actually a right dentary of *Leedsichthys*, 737mm long with most of its inferior and all of its posterior border missing. Most of the superior and anterior borders are present, although gaps do occur in both. In spite of the damage, much of the mandibular sensory canal is however visible amongst the striations (Patterson & Rosen 1977: fig. 32g), which it makes it the only skull element of *Leedsichthys* known to exhibit traces of a sensory canal (fig. 8.63c). A blade-like superior and inferior border to the bone thickens significantly in the mid-level. Although much of the medial surface of this specimen is (like the basiocciput) obscured by clay (and some consolidant), a prominent ridge can be seen posteriorly in the mid-third level of the bone, presumably for articulation with the prearticular. The anterior tip of the bone thins to an almost square end, with the internal surface showing a centrally radiating series of rays.

Only one **dermosphenotic** has been recognised from any specimen of *Leedsichthys*, a left, measuring 325mm x 205mm, in specimen BMNH P.12534 (fig. 8.64a,b). It seems to have all of its original perimeter, and to have retained its curvature without being crushed or broken, displaying large lateral line pores at the inferior part of its external surface (Grande & Bemis 1998). Medially, it forms a large groove to connect to the parietal. The anterolateral border forms the upper rear quarter of the orbit, indicating a possible orbital radius of around 100mm.

One **supramaxilla** has been identified, a left (fig. 8.65a,b), part of BMNH P.6930 (256mm x 129mm). Although its lower posterior border is damaged, its basic triangular shape is intact, along with its anterior articular surface with the maxilla.

A pair of **nasals** has also been identified as part of BMNH P.6930, the left measuring 238 x 115mm, and the right measuring 214 x 118mm (fig. 8.66a,b).

A possible lower jaw element has been identified in the northern Germany material (PMM 19.1-21.1, 23.1, 480mm long), BMNH P.66340 (330mm long, fig. 8.70a – previously misidentified as a nasal of the ichthyosaur *Ophthalmosaurus*, Neaverson 1935:p.240) and BMNH P.10156/3 (328mm long, fig. 8.70b). It may prove to be an **angular** or **supraangular** element (see Lehmann 1949: fig. 2), but further comparative analysis is required.

8.3.2.2 - Post-cranial:

Of all the meristic elements, two types were identified and removed from the range assessed under section '7' by their midline symmetry and virtual lack of antero-posterior curvature. The first is the **proximal radials**, that support the bases of the dorsal fin-rays. These bones occur in several specimens of *Leedsichthys*, but usually only in fragments. The best series of proximal radials occurs in GLAHM V3363 (fig. 8.67a), and consists of eight mostly complete elements, ranging in length from 627mm to 703mm (in both cases, 53mm wide at their superior edge). The longest element will be used for the description (fig. 8.67b,c). Both lateral surfaces display an 8mm wide vertical groove, that runs for the central two thirds of the height of the bone. Inferiorly, it becomes a part of around half a dozen vertical ridges that span the 19mm wide tip. At the superior end the proximal radial expands to its 53mm width, the groove disappearing in a smoothing of the surface, and the transverse section becoming more of a simple oval instead of the figure eight present throughout much of the length of the bone.

Fragments of other proximal radials also occur in BMNH P.6928 and BMNH P.6925.

The second meristic element with noteable lack of curvature is the anal fin and its supports. The anal fin has a ubiquitous presence throughout the pachycormids, its form being a basis for discrimination amongst the group (see Chapters 5 and 6, Appendices I and III). The **anal fin supports** in *Leedsichthys* are distinguished from other elongate meristic elements by being straight, with a thickened central ridge rather than a groove running down the centre, and with two thin flanges of bone running down the anterior and posterior surfaces. GLAHM V3363 has four such bones (fig. 8.68a), and BMNH P.6928 has a partial right element (395mm long, fig. 8.68b). The longest and most complete example, from GLAHM V3363, is a 617mm long right element, and will be used as the basis of this description. The anal fin support has a predominantly flat medial surface with slight indentations to receive its opposite and matching supporting element, and a lateral surface with a ridge 8mm high in relief. In spite of damage, it can be determined that the thin flanges are only absent from the distal 20% of the bone, reducing the width of the bone to 28mm from 57mm, ending in ridging, as noted previously for proximal radials and others. Typically, the bone resorption at the proximal end has resulted in a weakening and collapse of the periosteum in this region. This 50mm wide damaged area tapers slightly to a 41mm wide point after 53mm length, then slowly expands to 58mm wide over the next 200mm length.

8.4 - DISCUSSION

The poor preservation of *Leedsichthys* has been an obstacle to the understanding of its skeleton since its discovery was first reported (Smith Woodward 1889a). The variability of vertebral ossification in holosteans has been well-described elsewhere (Schaeffer 1967). Given the lack of any vertebral material in any of the approximately seventy known specimens of *Leedsichthys*, and the trend towards partial ossification of the vertebrae (e.g. *Pachycormus*) reaching its most extreme expression in *Saurostomus* (Smith Woodward 1916) and *Protosphyraena* (McClung 1908), it seems likely that the vertebrae simply were not ossified at all, but remained as unreplaced cartilage. This may in some elements have manifested as a delayed, perhaps paedomorphic, ossification, for example in the hyomandibula: during the excavation of one of these bones from the Star Pit in season 2002, it was noted that at the tip of the boss there was a 'crunchy' quality to the clay immediately in contact with the bone, which seemed 'unfinished', as though it was a

partially preserved calcified cartilaginous matrix, which disappeared when dehydrated (pers. Obs. 9/2002).

Although Webb & de Buffrénil (1990) suggested that a reduction in overall skeletal mass was less essential for large vertebrates, it seems to have been necessary for *Leedsichthys*, possibly as a strategy to deal with buoyancy problems. Although support of body weight is not a primary function of the skeleton in fishes, as virtual weightlessness means skeletal mass is not determined by a balance between strength and lightness (Berrios-Lopez *et al.* 1996), it is a factor in terms of manoeuverability with regard to accelerating and decelerating. As supporting tissues, notochord, cartilage and bone represent increasing rigidity, density and strength (Gosline 1971). This means that bone tends to be used to support muscle masses for swimming, and skeletal mass is more likely to be determined by the combination of water viscosity, foraging mode, propulsion mechanism and cruising velocity (as drag and thrust increase as the square of the swimming speed), than by support of body weight (Berrios-Lopez *et al.* 1996). For example, a different thickening of the spine is required for thrust-maximising and fast-turning ambush-predators, compared to pelagic plankton-feeders, in order to counteract the increased stresses (e.g. *Oreochromis nilotica*) to cope with the increased drag. On the other hand, increased bone strength actively reduces the effectiveness of the fins in manoeuvering. Fish retaining the most cartilage tend to have many vertebrae and be highly flexible, which can inhibit their locomotive efficiency (Lindsey 1978). Reduced ossification in the form of no scales (as seen in some other pachycormids, not just *Leedsichthys*) would reduce mass for more efficient swimming, but at the expense of compromising the defence of the body's organs and shape (Webb & Skadsen 1979). This can be addressed by the possession of body armour or a leathery skin (e.g. *Balistes*).

For *Leedsichthys*, the consequence of this reduced ossification strategy is a likelihood that elements of the skeleton are either preserved in fragments, or not at all, with cartilage a soft tissue unlikely to preserve except in the most unusual environmental circumstances (Allison 1988). Although intermittent episodes of euxinia have doubtless preserved many *Leedsichthys* specimens (Kenig *et al.* 2004), the only *Leedsichthys* specimen to be preserved in an exceptional preservation environment in the Oxford Clay (in Christian Malford, Wiltshire) is a fragment of a fin-ray (BMNH 46355, fig. 8.69). No exceptional detail or soft tissue traces were preserved in this specimen.

8.5 - CONCLUSIONS AND FURTHER WORK

Smith Woodward's 1889 descriptions of selected bones of *Leedsichthys* have been reviewed and revised. Further bone morphologies have been identified. Unidentifiable elongate meristic elements have been distinguished into discrete groups through analysis of their curvature, and suggested identifications made. This work on meristic curvature will be developed using CurveExpert and Eigenshape software packages to analyse degree of curvature in postcranial meristics of extant bony fish.

The current work is a prelude to the full description of the osteology, which will result from the final excavation and preparation of PETMG F.174, as part of a redescription of the taxon.

Chapter 9

"I often say that when you can measure what you are speaking about, and express it in numbers, you know something about it; but when you cannot measure it, when you cannot express it in numbers, your knowledge is of a meagre and unsatisfactory kind;"

Lord Kelvin, Chair of Natural Philosophy
University of Glasgow, 1883

Chapter 9

A Palaeobiological Model For *Leedsichthys*.

9.1 - ABSTRACT

Recent work has constrained previous estimates of the size of the Jurassic pachycormid *Leedsichthys problematicus*. Sizes and rate of growth have been found to be broadly comparable to the large chondrichthyan suspension feeders *Rhincodon typus* and *Cetorhinus maximus*. This current work begins to build an ecological model of *Leedsichthys* from these figures, in order to interpret as fully as possible its role within the Callovian marine ecosystem. Estimates of the length and mass of *Leedsichthys* are used in conjunction with skeletal evidence to constrain its likely locomotor abilities. These are then used to discuss its likely ecomorphotype, feeding behaviour and general palaeobiological/palaeoecological traits.

9.2 - INTRODUCTION

Leedsichthys is an unusually sparsely preserved and fragmentary fossil animal, making assembly of individual skeletal elements difficult, and reconstruction of its body even more so. This is primarily due to an apparent strategy to lighten its skeletal mass through a combination of reduced ossification (also noteworthy in certain other members of the Family Pachycormidae, in particular *Saurostomus* and *Protosphyraena*), which limited the number of bony elements that could potentially be preserved, and advanced bone resorption in many of the dermatocranial elements, leading to an extremely thin compact bone layer relative to the large size of the individual bones.

Building on the work of Martill (1986a), it was decided to attempt to scale a series of specimens of *Leedsichthys*, in order to estimate the animal's range of Standard Length (SL, *sensu* Holčik *et al.* 1989). Emerson and Bramble (1993) have drawn attention to the unreliability of skull components for scaling purposes, and so although there are specimens of *Leedsichthys* with large skull bones (BMNH P.6921 and BMNH P.10156), they lack post-cranial elements that could be scaled from, and so were excluded from scaling. A set of three appropriate specimens was selected: BMNH P.10000 (the 'Tail Specimen'), PETMG F174 ('Ariston') and GLAHM V3363 ('Big Meg'). Using another pachycormid (*Saurostomus* SMNS St.56982), Standard Lengths of 8046mm (from the pectoral fin length), 8913mm (an average of 8991mm and 8836mm from two aspects of the caudal fin) and 12345mm (an average of 11384mm and 13306mm for anal fin support and proximal radial lengths) were arrived at for the three selected specimens of *Leedsichthys*. Although

mass is generally better than length for scaling biological attributes from, length is better when the animals being compared are a similar shape (Schmidt-Nielsen 1977). As such, these lengths can be used to extrapolate biological characteristics from (Table 9.2), in order to construct a biological model of this animal, and assess its ecological role within the marine Oxford Clay ecosystem. In order to test the legitimacy of this approach for pachycormids, a scaled physical model was constructed, based on the body form of *Saurostomus*, modified by known sizes of skeletal elements of *Leedsichthys*. Although Wardle has noted a trend towards migration of the dorsal fin with increasing size of fish (1977), the dorsal fin has been kept in a neutral position to counterbalance the tail, Lighthill having observed that the higher the dorsal fin, the greater the minimisation of lateral recoil in response to caudal fin movement (1969: p.435).

The figures noted above are unusually large Standard Lengths for a bony fish, and indeed it may well be the largest genus known to have existed, particularly when there is evidence of specimens with larger skull elements (and more years of growth, see Chapter 7) than 'Big Meg'. Only the contemporary fish *Regalecus* comes close, and it has an extremely derived elongate bodyplan (Helfman *et al.* 1997), so its length does not imply the same degree of mass as *Leedsichthys*. The bulk of the work in this chapter will be an exercise in predictive ecology, following the example of Peters (1983), using these estimated and measured parameters to derive a model of the biological characteristics of *Leedsichthys*.

As noted by Peters (1983: p.183) increase in size is a prime indicator of ecological succession (*sensu* Odum 1969), reflecting a 'mature' ecosystem (Peters 1976). Large size correlates with increasing k-selection therefore arguably represents a greater quality and desirability of individual, large animals being worth more because they are rarer. Large animals have a greater control over the effects of their environment on them, as they are less likely to suffer predation, dessication, cooling, starvation and heating, are more mobile (thus able to roam over larger areas in search of food, shelter and breeding grounds) with greater visual power, have larger individual offspring, an increased learning capacity and increased morphological specialisation. They are also able to use energy more slowly than smaller animals, so that less food is required per unit of body weight, and indeed food of lower nutritive quality may be utilised (Hildebrand & Goslow 2001). The disadvantages are that they are therefore also more vulnerable to change, with a relatively small number of potential ancestors, so less heterogeneous genetically, showing lower rates of speciation and longer generation times.

The mass and volume of an animal are important for interpreting how it functions biologically. Calculation of exactly what this mass might be in an extinct animal can be complicated: a variety of techniques have been used by previous workers to attempt to reconstruct in three dimensions the volume and/or mass of an extinct (or problematic recent) animal. Hurlburt (1999) used an elliptical cylinder in modelling the pelycosaur *Edaphosaurus boanerges*, Luque & Aurioles-Gamboa (2002) used combinations of different geometrical shape combinations for sea lion pups, Seebacher used polynomials for dinosaurs (2001). Slicing the animal into component elements (Novitskaya 2000) has also been explored as a possible way forward, with Henderson (1999) creating CAD slices based on ellipses in order to estimate volumes and masses (including centre of mass), and Motani (2001) advocating the use of super-ellipses with body silhouettes in ichthyosaurs. From these volumes, surface area can further be derived, if the relationship is understood (e.g. Peters 1983 Appendix IIb).

Motani's method (2001) was useable for ichthyosaurs, because the Toarcian Posidonienschiefer frequently records soft tissue outlines for these reptiles, as well as preserving their skeletons. Similarly, specimens of *Saurostomus*, a pachycormid closely related to *Leedsichthys*, also from the Toarcian shales, can also record body outlines. As no specimens of *Leedsichthys* have been recovered with comparably preserved skeletons, this bodyplan was used (in a similar way to Bargo *et al.* 2000) as a template to build a three dimensional model, incorporating known skeletal elements from *Leedsichthys* specimens, and based primarily on the 'Tail Specimen' (BMNH P.10000). This specimen was chosen, because the well-preserved caudal fins offer valuable locomotory data that can be related to the other skeletal elements preserved (see 'Nutrition' section below). The volume and surface area of the model was then read by scanning and processing with RapidForm and MIMICS (fig. 9.1A,B), in order to compare with figures derived using Bainbridge (1961) and Webb's (1975) equations for estimating body mass and wetted surface area from the length of a fish (Table 9.1).

The small percentage differences between the calculated figures for the volume and surface area, and the figures predicted by Bainbridge's equations, support the validity of these equations (and, by implication, those of other fisheries workers based on length/mass) being used for pachycormid specimens.

Mass is a more useful term to deal with than volume for understanding an animal's biology, but conversion from one to the other is not straightforward for *Leedsichthys*: it is

evident from the reduced ossification of the skeleton of this animal (as signalled by the extensive remodelling of the compacta of most of the dermatocranium, and the large number of elements that appear to have remained as cartilage and not ossified) that this animal had a mass that was less than would be expected for a bony fish of this size. Although cartilage has a higher Specific Gravity (1.1) than seawater (1.026), it is around 55% that of bone (S.G. = 2) (Helfman *et al.* 1997), and although there is no indication whether or not this bony fish had a gas bladder or waxy esters or highly oily liver or increased fat content to counter its buoyancy problems (Magnuson 1978), it is clear that having more of a cartilaginous than a bony skeleton would have made it considerably easier and less energy-consuming for this animal to move through the water. The sunfish (*Mola mola*) is the most massive extant bony fish, and it has a secondarily derived cartilaginous skeleton, with reduced ossification (Helfman *et al* 1997, Freedman & Noakes 2002). The negative buoyancy of a fish is largely due to the mass of its skeleton, and by not ossifying much of this skeleton, and reducing the density of the bones that did form (through a highly porous cortex dominating the interior of the bone with only a thin external compacta), the fish would significantly reduce its negative buoyancy problem. The more cartilaginous a fish's skeleton, the longer that it can grow without compromising its capability for lift, as skeletal mass grows with the cube of length, whereas lift grows as the square of the fish's length or the cross-section of the muscle available to power swimming. Put another way, "the length at which cartilaginous fishes run out of lift is longer than bony fishes." (Summers, pers. Comm. 7/3/2006).

Given the demonstrated applicability of the equations of Bainbridge (1961) and Webb (1975), one can approximate the mass of the BMNH P.10000 specimen of *Leedsichthys* as some 7,000kg (Tables 9.1 and 9.2), which although small compared to the 12,000kg recorded for the basking shark *Cetorhinus maximus* and 15,000kg for the whale shark *Rhincodon typus*, is significantly larger than the record for the most massive (1,500kg) extant bony fish, the sunfish (*Mola mola*) (Freedman & Noakes 2002).

It is another indication of a broader strategy of combatting negative buoyancy, that the pachycormids are defined by their characteristic large pectoral fins, leading one early author to describe them in terms that closely resemble the description of an ipnopid 'bottom-walking' fish (Smith Woodward 1916). Although pectoral fins with such a large surface area might be interpreted as possible tools for 'non-body' swimming, it is clear that regardless of whether or not these fins might have been able to rotate, they could not (given their rigid, branched, unjointed and unsegmented nature) generate the 'feathering'

or other necessary rowing motions required for this activity (Blake 1983). This is in contrast to the hinged pectoral fins of the sturgeon (Wilga & Lauder 1999) whose function was misrepresented as a lifting surface, when the ability to alter the surface of the fin actually aided manoeuvering far more than it generated lift. What appears more likely when one regards the pectoral surfaces of *Leedsichthys* as 'lifting wings' (Webb 1975) is that these large pectoral fins were required in order to generate sufficient passive lift from the fish's forward motion for it to be able to maintain neutral buoyancy. Species with large pectoral fins and thus a greater lifting force relative to Standard Length, should have a lower minimum swimming speed than those with small pectoral fins (Blake 1983: p.157). This was also noted by Gero (1952) in terms of the power loading decreasing with increasing body mass for a given velocity, because the power varies with the surface area as the weight of muscle varies with the body mass. Less lift is required to counter sinking in fish that are smaller or that have an overall density closer to that of their habitat (Magnuson 1978). Although we lack specific data on relative lift from the keel and the lower surface of the body of *Leedsichthys*, two apparently *in vivo* position pectoral fins indicate (span of 3541mm and chord length of 385mm) an extremely high aspect ratio of over 9, thus giving a higher ratio of lift to drag over a similar fish with shorter pectoral fins (Magnuson 1978). This is consistent with the observation that pectoral fins grow allometrically to lower fin loadings (Magnuson 1978 and similarly noted for plesiosaur paddles in O'Keefe & Carrano 2005). Conversely, as larger animals tend to travel faster than smaller ones, and lift is a result of the square of the velocity, it is found that although lifting fins are comparatively larger on larger animals, they tend to not be as enlarged as one would expect for the size of the animal (Vogel 1994).

Although Hildebrand & Goslow (2001) have commented that "aquatic giants support their bodies effortlessly by flotation", these fishes evidently employed a series of strategies in order to resolve their buoyancy problems.

9.3 - DISCUSSION

The following seven sections discuss different aspects of the ecology of this animal, using the seven measures of life (movement, respiration, nutrition, irritability, growth, excretion, reproduction – M. Faithfull, pers. comm. September 1979) as a structure. Much of the discussion is, of course, theoretical, applying knowledge and patterns derived from contemporary marine animals (Peters 1983) to interpret the comparatively small quantity of data that can be extracted from the fossil remains of this animal and its environment.

The main focus of this chapter is the feeding requirements of *Leedsichthys*, which are intimately linked to the locomotory abilities of the animal.

9.3.1 - Movement

Gray (1961) observed that a "complete picture" of the locomotory activity of any vertebrate would require a precise knowledge of the changes in length and tension of "a very large number of muscles and an accurate knowledge of their anatomical arrangement" (e.g. Nursall 1956), something that is beyond our current ability to reconstruct in *Leedsichthys*. Motani (2002b) has, however, noted that the swimming capabilities of extinct marine vertebrates reflect their behaviour, therefore being able to estimate the swimming speeds of extinct marine vertebrates is an important step towards understanding their biology. In water, the primary means of propulsion is undulatory (Holwill 1977), with ciliary propulsion only effective at a size where viscous forces are dominant (Lighthill 1970, Sleigh & Blake 1977). For most fish this undulation is focussed on the tail, and indeed this can be used to infer speeds, even for extinct aquatic animals, provided one knows the length of the fish in question (Massare 1988). The length estimates already derived will serve in this regard.

In addition to length, another important control on locomotion is an animal's stiffness, which is particularly relevant to fish as variably ossified in their vertebrae as pachycormids are. Fish that retain the most cartilage have many vertebrae and are highly flexible (Lindsey 1978). Long & Nipper (1996) regarded non-mineralised or unossified vertebral centra as equivalent to three hundred vertebrae in their study on body flexibility in undulatory propulsion, as they were presumed to have maximal flexibility, with the increasing numbers of vertebrae meaning an increased maximal body curvature. In the absence of ossified centra, stiffness could still be conferred on the body by the use of the musculature, enabling the propulsive wave to travel faster down the body. The body of the fish is already under transmural pressure (Dubois 1977), and its flexibility can be varied if the musculature is concentrated anteriorly and thinned posteriorly (Webb 1975). Batty & Domenici (2000) noted that animals larger than 0.4 metres would start to experience problems with acceleration, so some have increased body stiffness (e.g. tuna) at the expense of limiting their manoeuverability (although this is compensated for in the tuna by group foraging behaviour). Long (1995) noted that *Acipenser transmontanus* could double its speed simply by increasing its midline flexure while maintaining the same tailbeat frequency. The degree of flexibility present in the body clearly has implications for the

nature of the undulatory movement in *Leedsichthys*: was the rigidity of this animal's body compromised by the reduced ossification of its vertebral column? It is worth noting that many of the characteristics of the body of *Leedsichthys* in terms of discontinuous median fins, reduction in number of fins and discrete enlarged caudal with a narrow-necked caudal peduncle, are seen as part of a long trend towards decreasing body flexibility (Webb 1975).

The reduced ossification of the axial skeleton is a trend that runs counter to most locomotor-related actinopterygian developments (Webb 1982). This has different impacts on the fish's movement, depending on the level of swimming the fish is engaged in, and this is determined by the length of duration of the swimming activity (Magnuson 1978):

1) Cruising or sustained swimming, for longer than 200 minutes (e.g. preferred speeds of negatively buoyant fish in order to gain adequate lift; migrating or foraging behaviour) (Webb 1975) – dependent on the fish being able to maintain the function of its oxygen supply and waste removal systems, range can be around 0.5-5.0 lengths per second for scombrids and cetaceans. This tends to maximise range and/or energy (Blake 1983), for example the 'burst-and-glide' (or 'beat-and-coast' McNeill Alexander 1989) pattern of movement for non-rigid body swimmers can reduce energy expenditure by 50% and potentially triple range achieved by negatively buoyant fish (Webb 1975). Small fish do not benefit from burst-and-glide as their bodies are comparatively rigid, and stiff-body gliding drag is very similar to swimming drag, so there are no real energetic benefits from gliding for these fish. But the larger the fish, the more helpful burst-and-glide is as a technique of reducing energy expenditure (Vogel 1994). There are also significant advantages in energy efficiency and range for negatively buoyant fish schooling together, with wing tip vortices generated from pectorals creating an 'upwash' for other members of the school.
2) Prolonged/steady (optimally efficient) swimming, for between 20 seconds and 200 minutes.
3) 'Fast starts' are usually bursts of acceleration of less than a second in duration (Domenici & Blake 1997), dependent on immediate energy reserves (Webb 1975), although larger fish perform longer fast starts because their minimum muscle contraction time (which in turn affects their burst swimming speed) is larger (Domenici & Blake 1997). Fast starts can be C-starts (mainly used by predators attacking prey – sometimes called L-starts, Webb 1976) or S-starts (mainly employed by escaping prey), depending on the shape that the fish's body is thrown into at the start of the manoeuvre. Large fish can also effect short duration fast-starts at small angles of turn

in order to minimise the amount of time involved in the process. Batty & Domenici (2000) noted an advantage of not having a stiff body was an improved fast start ability.

Webb & Skadsen (1979) noted a reduction in skin mass (including loss of scales) with increasing body size in bony fishes. If *Leedsichthys* did have any scales, none have been preserved in the fossil record, and indeed the evidence from well-preserved Holzmaden pachycormids from the Toarcian is that there is a trend towards reduced scale-cover across the taxa, possibly another aspect of the paedomorphic trend across Family Pachycormidae that appears to correlate with increasing adult-size. This would seem to make it more likely that *Leedsichthys* simply (like other pachycormids larger than a metre in Standard Length) did not have any scales. If one also bears in mind the tendency for fish to develop increased armour and scales due to the intensity of predation in the marine environment in contrast to their freshwater equivalents (Baker *et al.* 1995), this is an unusual strategy. Webb speculated that scale-loss might be an evolutionary strategy to aid fast-start and unsteady swimming behaviour by reducing resistance (Webb 1982). In contrast, Blake (1983) specifically referred to the development of scales as small fish increased in size and their body movements approached critical Reynolds Numbers, as a means of aiding with the transition to turbulent flow, and suggested that 'eye fairings' arose in some older fish to facilitate boundary layer separation.

9.3.1.1 - Size

An animal's potential velocity is strongly controlled by its size: the larger it is, the faster it can go and the broader its range of speeds (Peters 1983: Fig.6.4). As Schmidt-Nielsen remarked (1984), "speed is undoubtedly related to the body size of the fish; large fish swim faster than small fish, but the comparison looks different depending on what scale we use." Length rather than mass is the key measurement for understanding fish movement, because although the amount of power available for a fish to move is related to its mass (and thus to the cube of the fish's length), the resistance of the fish varies with the surface area of the body and therefore with the square of the fish's length. As such, speeds are best expressed in terms of body length (Gray 1968). Also, length is the characteristic measure of size for a fish because it is the scale measure for the Reynolds number. This number is an expression of Reynolds Law (which together with Froudes Law make up the Laws of Similitude to describe the action of inertial gravitational and viscous forces on objects moving in a fluid, Webb 1975) indicating the relative influence of viscous and inertial resistance components on an animal (Webb & Johnsrude 1988). The Reynolds number is

calculated from the product of the speed and the length of the animal, divided by the kinematic viscosity (dynamic viscosity/density, Videler 1993) of the fluid (Lighthill 1969, Wu 1977). For *Leedsichthys* specimen BMNH P.10000, with an estimated length of 8913mm, assuming a range of velocities from 1 ms^{-1} to ten body lengths per second for possible burst swimming, the Reynolds numbers range from 8.1 x 10^6, to 7.2 x 10^8. The important indication from this is that an animal of this size, even moving at relatively slow speeds (just over 0.1 body lengths per second) through the water, is entirely governed by inertial forces, and not viscous forces (Batty & Blaxter 1992).

Various fish muscle characteristics increase with fish size and can be directly related to the length of the animal. As a fish increases in length, its maximum force, power and velocity all increase. The maximum amplitude of movements are proportional to the length, but the period of the propulsor movement (in this case the tail) is proportional to $length^{\sim 0.5}$, and the lateral velocity of the tail is proportional to $length^{\sim 0.6}$ (Webb & Johnsrude 1988).

Absolute swimming speed increases linearly with tailbeat frequency (Webb *et al.* 1984), so that for any given frequency, larger fish swim faster than smaller fish as a result of increased length of muscle fibres, giving more sarcomeres in series (Goldspink 1977) with more slow muscle fibres and longer stride duration. Muscle efficiency increases with size (Webb *et al.* 1984). Regardless of the size of the fish, the distance moved for one tailbeat is always the same proportion of its bodylength (Schmidt-Nielsen 1984), a 'stride' generated by one tailbeat being the equivalent of 0.7 x Standard Length of the fish (in the case of *Leedsichthys* BMNH P.10000 with estimated length of 8.913m, the stride is 6.24m) (Wardle 1977, although see also Wardle & Videler 1980). However, the maximum possible frequency of tailbeats decreases with the increasing length of the animal (Gray 1957) as this is limited by the contraction rate of the white (anaerobic) muscle (Webb 1976). The drag, the specific (body lengths per second) speed and the specific propulsive wavelength (Webb 1977) also decrease with increasing Standard Length. The thrust generated by the tail is proportional to the tailbeat frequency, the amplitude, the trailing edge and the swimming velocity (Long & Nipper 1996).

9.3.1.2 - Mode Of Movement

Following on from the work of Breder (1926), Webb (1975) noted in his classification of grades of motion in fish that "Swimming modes themselves are merely verbal descriptions of swimming patterns that may now be expressed in a relatively concise mathematical

form, and perhaps ultimately in terms of fish geometry alone." With the partial remains of a fossil fish, an attempt will be made to use the morphology of the animal to ascertain its likely swimming pattern. As Nursall (1958) noted, the shape of the caudal fin can be used to draw conclusions about the mode of life of a fossil fish.

Although there is a continuum (Webb 1982) of swimming methods (Videler 1993), the principle division in types is between median/paired fin propulsion (Webb 1978), and body/caudal fin undulation (Webb 1975). The former category requires the fish to be able to pass waves along their fins or scull with them like oars (Blake 1981), operations that the rigid, branched and unsegmented structure of the pectoral fins of *Leedsichthys* could not perform. In the latter category (body/caudal fin undulation) three major modes are noted (anguilliform, carangiform and ostraciform Moyle & Cech 2000) that reflect a decrease in the relative length and flexibility of the tail, or can be viewed as a trend towards decreasing body flexibility (Gray 1968).

Fish swimming in an anguilliform mode (e.g. *Anguilla*, *Pholis*, pleuronectids) will be flexible and elongate, with continuous dorsal and/or ventral fins, a low aspect ratio tail if one is present at all (Blake 1983), undulating their fins at low speeds and throwing the whole body into lateral waves in order to propel themselves forward at higher speeds (Lighthill 1970). Carangiform swimmers (e.g. *Clupea*, *Caranx* and *Scomber*) will have a relatively narrow caudal peduncle with a stiffer tail 'scooped out' to give a sweptback planform (see Webb 1975: p.27 Fig. 22c) and around half the body involved in the propulsion wave, which is concentrated in the posterior third of the body (Lighthill 1970). Within this style a special category is noted, that of carangiform with semilunate tail, also referred to as 'thunniform' (e.g. *Euthynnus*, *Phocoena*, *Balaenoptera*), reflecting the high aspect ratio tail and fusiform shape of its practitioners, which has evolved separately in lamnid sharks, percomorph teleosts, cetacean mammals and ichthyosaurian reptiles (Webb 1975). The third and final swimming mode is ostraciform (e.g. the Tetraodontiformes), where the body is rigid and not streamlined, usually armoured, and the flexion that occurs at the caudal peduncle is designed for 'sculling' locomotion with a small isocercal caudal fin (Moyle & Cech 2000).

In dismissing the use of aspect ratios as a phylogenetic tool, Nursall (1958) noted a pattern of swimming ability, tail-form and musculoskeletal changes varying together along different evolutionary paths, in four discrete groups defined by character combinations broadly similar to those present in the swimming modes already referred to. The first

group, exemplified by an eel, produced large amplitude and low frequency body undulations, with a flexible vertebral column of many short vertebrae, thick muscular body and thick caudal peduncle with a rounded caudal fin of negligible aspect ratio. The second group (e.g. perch) produced moderate amplitude with fairly high frequency undulations, with a flexible vertebral column of between 24 and 100 short vertebrae, and a narrowed muscular caudal peduncle with a flexible forked caudal fin of intermediate aspect ratio (between 2 and 4). The third group (e.g. tuna) produced a wave of low amplitude but very high frequency undulations, with a stiff perhaps elastic vertebral column of long vertebrae (between around 30 and 45) with a slim non-muscular caudal peduncle supporting a tail of high aspect ratio. The fourth group were defined as the plectognaths (or Tetraodontiformes), with a short vertebral column of 14-20 vertebrae with limited flexibility, poorly developed lateral musculature and a flexible tail fin of low or negligible aspect ratio.

If one accepts that the continua represented by the schemes of swimming mode and character combinations presented above reflect real patterns of fish movement that can be applied to fossil representatives, then it is necessary to determine to which group *Leedsichthys* might belong. According to Lindsey (1978), the lack of ossified vertebrae mitigates strongly in favour of an anguilliform style with many vertebrae (as with most sharks), as cartilaginous vertebrae are assumed to equate with a body of poor rigidity, and this rigidity is key to the speed with which the undulatory wave travels down the body of the fish (Long & Nipper 1996), with a wavelength less than 1 signifying anguilliform mode, and a wavelength greater than 1 signifying carangiform. However, not all sharks, in spite of their cartilaginous vertebrae, move in an anguilliform mode. Webb (1990) regarded the two largest suspension feeding sharks (*Rhincodon* and *Cetorhinus*) as thunniform. Long & Nipper (1996) reviewed the use of the body musculature to aid the stiffness of the body, in addition to the transmural pressure (Dubois 1977, Randall & Daxboeck 1984) that the body is under, and demonstrated (their Fig. 2) that the wavelength range of taxa often crosses the notional divide between anguillifom and carangiform modes (Long & Nipper 1996).

Blake (1983, chapter 7) noted that fish designed for steady cruising performance are characterised by a high aspect ratio forked caudal fin. The development of the caudal fin into a "...herring-like...pair of highly sweptback wings" should reduce drag without significant loss of thrust (Lighthill 1970). This is because the Froude efficiencies of the tail are retained if the span is increased while reducing the area and thus the effective mass

of the tail (McCutchen 1977), reducing resistance and producing an associated gain in speed (Lighthill 1970). In contrast, slow-swimming fishes are characterised by a low aspect ratio and sometimes spade-like tail (Blake 1983) resulting in a decrease in the thrust coefficient and the hydromechanical efficiency (Chopra 1975). The most extreme form of this trend in slow-swimming tail design has a rounded leading edge and a sharp nearly straight trailing edge, effectively turning it into a thin rectangular wing (Chopra 1975).

The tail of *Leedsichthys* specimen BMNH P.10000 is 2740mm high, with a surface area of 1.745m^2 and a moderately high aspect ratio (Vogel 1994) of 4.32, indicating an animal with a steady cruising speed (see Chapter 7). The well-defined tail with its sweptback planform shape is a compelling argument for this animal to have moved in a carangiform/thunniform mode rather than an anguilliform one (Gray 1968), and to have naturally been associated with Nursall's third group (exemplified by the tuna, with possibly elastic vertebral column) out of the four that he presented (Nursall 1958). It also implies (Lighthill 1970) that *Leedsichthys* would have had a significant increase in the depth of its body (including dorsal and anal fin lengths, to approximately the height of the caudal fin) anterior of the caudal peduncle and for much of the anterior half of the body, in order to reduce recoil effects. Lighthill (1969) looked more closely at the convergence on the form of the lunate tail by many groups of fish and other vertebrates, regarding it as a culmination in the enhancement of speed and propulsive efficiency (Lighthill 1970), and suggested that this might be because this particular shape of tail readily sheds vertical vortex rings of a near circular shape, carrying a large amount of momentum and thus increasing power effectiveness (Lighthill 1969). He noted that these tails typically gave a solution to the equation π x fish standard length/span of caudal fin of the order of 10, and indeed the figures calculated for BMNH P.10000 give 10.21 (3.14 x 8.91/2.74 = 10.21, which perhaps also serves as some independent support for the value of the estimated length derived for this specimen). Lighthill also notes that being an active swimmer with this tail-form reduces buoyancy problems, and fast-moving sharks (such as *Rhincodon*) would move in "practically the same carangiform mode" as the fastest of the teleost fishes with a lunate tail (Lighthill 1969).

9.3.1.3 - Estimation Of Speeds Of *Leedsichthys*:

A number of methods have been developed for calculating ranges of velocities of fish with particular physical parameters, from length (e.g. Parsons 1990), to tail form, to body mass. These can be applied to extinct animals, assuming that the general conditions that govern the fish that the work was based on are valid for the extinct forms, which seems in general

to be reasonable. However, it should be noted that several of the methods of deriving this data are temperature specific, which is hard to constrain for the environment of *Leedsichthys*, yet is important for speed of muscle contraction/tailbeat frequency (Batty & Blaxter 1992) and general metabolic rate (Schmidt-Nielsen 1984). Palaeotemperature analyses of invertebrate remains (ammonites, belemnites and *Gryphaea*) as well as *Leedsichthys* have yielded a range of temperatures from 20-29 degrees centigrade (Anderson *et al.* 1994) in the Peterborough Member of the Oxford Clay, with estimates for the bottom waters from aragonite of 15 degrees centigrade (Hudson & Martill 1991). It should be noted that the environment would have consisted of a variety of temperatures at a variety of depths in the water column throughout the year, which may well have overlapped with the experimental temperatures used to derive speeds from contemporary fish. Although all that can be done to examine this extinct fish is to apply these assumptions to the model to see if it produces reasonable results, it must however be remembered that *Leedsichthys* as (apparently) the largest bony fish known to have existed, may well have been governed by subtly different rules, conditions and assumptions.

Adapting other work to calculate such velocity ranges for *Leedsichthys* presents certain problems: few aquatic vertebrates exist today with the length and mass estimated for *Leedsichthys*, and as noted by Schmidt-Nielsen (1984) "allometric equations cannot be used for extrapolations beyond the range of the data on which they are based." If one did not note this problem, then one could apply Blake's (2000) observations on crossover speed, and calculate the speed at which *Leedsichthys* would have begun porpoising behaviour simply by extending the curves in the graphs presented, which one instinctively must believe to be a highly unlikely behaviour for this animal to have undertaken. Similarly, applying allometric equations with empirically derived constants that relate to a narrow range of tested swimmers, without justification for similarities between those observed animals and *Leedsichthys*, would result in meaningless values. However, if graphs present straight line relationships against length or mass for a range of swimming animals, it is a worthwhile exercise to extend those straight lines and see where *Leedsichthys* would fall if the conditions that constrain the graph did indeed apply to it, to compare with estimations of speed arrived at from other sources.

In this regard, Hunter & Zweifel's elegant equation is unfortunately dependent on being able to determine a fish's minimum swimming speed, so cannot be used for *Leedsichthys* (1971). Wardle reviewed the effects of size on the swimming speeds of fish, and presented a plot of burst swimming speeds as related to Standard Length (Wardle 1977: Fig.5). A

straight line emerges on the graph, which if extended would give a reading for an 8913mm long fish of around 49ms^{-1}. The data used to construct the graph are, however, limited to fish less than one metre in length, for which the straight line part of the graph only applies above 0.4 metres in standard length. Given the reduced contraction time of anaerobic muscle for maximum velocity with increasing length (Altringham & Johnston 1990) or mass (Webb 1976, Wardle & Videler 1980, Altringham & Young 1991; although note also evidence for some utilisation of red muscle fibres for higher speeds in teleosts, Johnston 1981) and the increasingly significant virtual mass of water that has to be accelerated with the fish (10% of the mass of the fish, Gero 1952; 20% of the mass of the fish, Webb 1975), this figure is highly unlikely to reflect an achievable velocity by this fish, but may reflect a rate of acceleration over a fraction of a second. This contention is supported by Bonner's 1965 work (cited in Peters 1983) showing maximum velocity against body mass, which indicates a maximum of 11ms^{-1} for an animal of the estimated mass of BMNH P.10000. In marked contrast, Webb & de Buffrenil (1990) found a relationship for the speed of large (over 0.5 metre in length) aquatic vertebrates proportional to (Standard Length of the vertebrate)$^{0.4\text{-}0.6}$, which produces a series of maximum sprint speeds (sustainable for at the most only a few seconds) proportional to 2.40-3.72ms^{-1}. Although lacking the constant from the power formula that would more usefully constrain this figure, this range does offer a more realistic idea of the possible maximum speeds of this animal. Similarly, Bainbridge's (1961) formula (which tested satisfactorily for both small fish and large whales) for the burst speed of a hypothetical fish where the propulsive muscle was 50% of its body mass ($V_{turb} = 62.35L^{0.39}$; the equation for turbulent flow is used in preference to the one for laminar, as the size of the animal makes laminar flow highly unlikely), produced a burst speed figure of 8.82ms^{-1}. As the question of the proportion of the body mass that would be muscular is problematic for *Leedsichthys*, given the uncertainties surrounding the bone/cartilage ratio in its axial skeleton, this seems to be an unsafe method to employ for this particular fish.

Of more interest and relevance than maximum speeds, which are utilised by an animal for only a very short proportion of its daily life (e.g. escape from predators), are optimum speeds, which can be defined in a number of ways relating to the lowest cost of transport (Domenici & Blake 2000). Ware (1975) assessed the optimal swimming speed of pelagic planktivores in terms of calorific intake. Weihs (1973) defined optimal fish cruising speed as being when the rate of energy expenditure for the swimming velocity was equal to the standard resting metabolic rate, while reviewing migratory fish (in other words, the total metabolic rate was equal to double the standard rate, Webb 1975; Weihs 1981). Weihs

(1977) noted that preferred or optimum cruising speeds (in terms of energy expenditure) varied slowly with animal size, so that whales and large sharks had relatively smaller swimming speeds (in terms of body lengths per second) than fish that were smaller in Standard Length. His plotted dataset was large enough to read a value for *Leedsichthys* of around 1.3ms^{-1} from the graph (Weihs 1977: Fig.1). Peters (1983) cited an equation used by Ware (1978) ($V = 0.39W^{0.136}$) to predict the optimal speed of a fish based on its mass in kilogrammes from which the figure 1.30ms^{-1} emerged. Weihs & Webb (1983) independently derived an equation that predicted optimal constant speed from length from a perspective of propulsive efficiency, which had identical exponent values to Ware's 1978 work (i.e. 0.43). In contrast to Ware, they were able to state the value of the constant in the power formula as well, giving a figure of approximately 0.5. If one applies the estimated length of *Leedsichthys* (8913mm for BMNH P.10000) to this equation, the figure of 1.28 ms^{-1} emerges as the theoretical optimum constant speed for specimen BMNH P.10000. Weihs & Webb went further (1983), to develop a variant of the equation to establish optimum feeding speed for suspension-feeders, such that the ratio of energy intake to energy expenditure was at an optimum value. In this form, the constant changed from 0.5 to 0.69, producing a theoretical optimum feeding speed for *Leedsichthys* of 1.77ms^{-1}. This will be utilised below in an attempt to assess some of the suspension-feeding constraints on *Leedsichthys*. This elevation of speed during feeding above optimum cruising speed is consistent with Durbin's (1979) observations on suspension-feeding menhaden, and is in contrast to the foraging speed of a fish being described as 20% of its critical speed (Webb & Gerstner 2000). Dabrowski *et al.* (1988) explored the relation between size and the optimal feeding speed of a marine planktivore, noting that for efficient feeding a balance had to be struck between ingesting plankton as quickly as possible and keeping the increased metabolic rate resulting from an increased speed as low as possible.

The equations and graphs used thus far have been derived from observations on a wide range of extant aquatic vertebrates. Estimation of optimum velocities in extinct aquatic vertebrates was pioneered by Massare (1988), who calculated the sustained swimming speeds of Mesozoic marine reptiles using body shape, estimated drag and estimations of energy available through metabolism. The technique produced overestimates, and was subsequently refined by Motani (2002b). In presenting his results, Motani showed Mesozoic marine reptiles in terms of three possible metabolic models, that of turtles, tunas and cetaceans/pinnipeds (2002b). If one extends the straight line on his graph for tuna (Motani 2002b, Fig.2B) to a fish of SL 8913mm, the graph indicates a value close to 2.0ms^{-1}. Although indications of an elevated metabolism have been noted previously in

the histology of *Leedsichthys* (Bardet *et al.* 1993, see Chapter 7), this value for the sustained swimming speed of *Leedsichthys* may be an overestimation, given that tuna have exceptionally high metabolic rates for bony fish. Motani (2002a) also provided an alternative method for predicting optimum cruising speeds for ichthyosaurs, based on caudal fin shape, size and stride length (6.42 metres for *Leedsichthys* BMNH P.10000, as stride length = 0.72SL, Videler 1993). Humphries (pers. comm.) used this model to estimate optimal cruising speed based on the assumption of constant and optimal Strouhal numbers 0.25-0.35 for optimum thrust production (Taylor *et al.* 2003). Using this model, BMNH P.10000, estimated at 8913mm Standard Length with a tailspan of 2740mm, would have an optimum velocity of 4.11ms^{-1} at 0.65Hz. A further model based on the Strouhal range for optimum thrust production gives a range of velocities proportional to 0.99-1.38ms^{-1} (as $V \alpha 0.2L^{0.25}$). The figure of 4.11ms^{-1} does seem unusually high for an optimum speed, and stands out from the other methods used, which seem to concentrate instead on a range between 1.28ms^{-1} and 1.30ms^{-1}. This would seem to lend support to the use of Weih's & Webb's methodology (1983), which also produced the figure of 1.77ms^{-1} as an optimum suspension-feeding speed. This value may seem high compared with observed basking shark feeding speeds within the range of 0.7-0.94 ms^{-1} (Sims 1999, Eckert & Stewart 2001) and whale sharks of 0.28 ms^{-1}, but lies well within the range of 0.83-2.5 ms^{-1} for balaenid whales feeding (Werth 2004).

In order to effectively assess the likely respiratory abilities and requirements of a fish the size of *Leedsichthys*, it is important to review some other relevant physiological attributes that the animal is likely to have possessed. A fish with a body mass of around 7,000kg will have a far more stable body temperature than a smaller fish, as both heating and cooling rates vary directly with body mass, but the half-time for cooling is significantly longer than the heating half-time, so there will be a tendency for the fish to retain rather than lose its body heat (Spigarelli *et al.* 1977). Given that the conductance for fish (using animals up to 10kg in mass) is given by $c_{fish} = 5.3W^{0.56}$, this would otherwise mean a loss of over 750 watts per degree centigrade for BMNH P.10000, but the large mass of this particular fish would significantly offset this thermal drain from its body.

Hughes (1977) presented an equation for a number of teleosts, stating that teleost heart mass = 0.0015mass(in grammes)$^{1.07}$, which would indicate a 31.6kg heart for BMNH P.10000. Helfman *et al.* (1997: p.144) referred to a slightly different equation (0.002mass$^{1.03}$), which produces a figure of just under 22.5kg. Although these may seem

excessive figures (particularly as the individual animals sampled for Hughes' equation had no mass greater than 1kg), it is worth bearing in mind that as blood viscosity appears to vary directly with body mass, so the heart would need to expend more energy in order to effectively circulate the blood around the body without allowing unsupported metabolic function to occur at the extremities of its body, as the blood pressure needs to be kept low in the gills for efficient gas exchange to take place (Hughes 1977, 1984). It has also been argued by Kiprianou that fish hearts, with only one set of chambers, can be regarded as "inferior" in design compared to cetaceans, this being given as a reason why fish do not grow as large as whales (Villazon 2002), and therefore a large bony fish might well need a comparatively large heart for its size in order to function effectively.

The quantity of energy expended in aquatic locomotion does not solely rise as a function of speed (as with terrestrial animals), but also as a function of body size, as the drag forces on the body increase with speed (Johnston 1981). The drag forces on a swimming fish are a combination of friction drag (the force required to overcome the viscosity of the liquid through which it is moving) and pressure drag (related to the displacement of water by the frontal area of the fish). The friction drag can be calculated for *Leedsichthys* specimen BMNH P.10000, using the equation:

$$\text{Friction drag} = 0.5 \times (\text{density of the fluid}) \times (\text{wetted surface area}) \times (\text{speed})^2 \times \text{drag coefficient}$$

The density of sea water at 35% salinity and 15°C is 1025 kgm^{-3} (Videler 1993), and the wetted surface area is assumed to be given by 0.4 x $length^2$ (Webb 1975). The drag coefficient varies with the Reynolds number, so that it decreases with increasing speed/Reynolds number, until it eventually 'bottoms out' with large enough Reynolds numbers (Schmidt-Nielsen 1984) at 0.004 (e.g. seals, penguins, large fish) (Vogel 1994). Given the flow regime that *Leedsichthys* is likely to have travelled in, it therefore seems reasonable to also use 0.004 as the drag coefficient for it. Applying the two extremes of estimated optimal constant speed for this fish ($1.28ms^{-1}$ and $4.11ms^{-1}$) to this equation thus produces friction drag figures of 106.74 g wt and 1100.50 g wt respectively.

In dealing with cetaceans, Slijper (1961) demonstrated that a variety of body shapes and cross-sections could travel through a fluid at a given speed, regardless of variations in scale. A streamlined fish body will have a low pressure drag, and the total drag will be roughly equivalent to 1.2 x friction drag coefficient, which varies directly with speed. As

metabolic rate is equal to the power required, it is equal to the force of drag multiplied by the speed. As drag is proportional to speed squared, the metabolic power or rate increases with the cube of the speed (Schmidt-Nielsen 1984). So metabolic rate rises with activity (Herrmann & Enders 2000), although the relative cost of swimming decreases with body size (Helfman *et al.* 1997).

Because the drag forces on the swimming body increase with speed, burst or sprint swimming requires proportionally more effort than sustained swimming. In addition to recapitulating Bainbridge's (1961) guidelines for calculating the body mass and surface area of a fish from its length (mass = $0.01L^3$, wetted surface area = $0.4L^2$), Webb also provided equations indicating the proportions of body mass that constitute cruising/sustained swimming muscle (0.025 x mass, equals 175kg for BMNH P.10000) and sprint muscle (0.5 x mass, equals 3,500kg for BMNH P.10000) for bony fish (Bainbridge 1961, Webb 1975). Johnston (1981) offered a more critical breakdown, pointing out that the number of distinct muscle fibre types in fish varies between two and five (depending on species), and the slow red fibres that alone support sustained swimming in holosteans, chondrosteans and 'primitive' teleosts, make up between 0.5 and 29% of the total muscle, with the highest percentage belonging to active pelagic fishes (like the scombrids), the red muscle fibres forming a thin superficial or internal strip (Johnston 1981). The fast white muscle fibres are solely for short periods of burst swimming. Some fish undergoing seasonal starvation will break down some of these muscle proteins. Similarly, Webb & Johnsrude (1988) noted that calculations (for expected speeds) based on myotomal muscle were weak, as they failed to take into account the huge variation in muscle proportion, even on an intraspecific basis (e.g. 30-60% in some cottids). With increasing fish size, the disparity in observed and predicted velocities and accelerations increases. Webb & Johnsrude speculated that sprinting in large fish is dependent on the summation of a few (rather than single) muscle twitches, in order to provide increased speed and power and overcome the problem of declining sprint performance with increasing size (Webb & Johnsrude 1988, Altringham & Johnston 1990, Altringham & Young 1991). As has been noted, there is uncertainty over the proportion of *Leedsichthys* skeleton that was actually cartilage as opposed to bone, which means that figures based on a percentage of total body mass have an unknown margin of error. However, they will serve as a fair approximation until more data becomes available to further constrain the model (potentially through construction and testing). On this basis, Webb's model for expected maximum muscle power output in cold water fish, and propulsive thrust for warm water fish cruising, both give figures close to 10^{11} ergs/second for a fish of the mass of BMNH P.10000 (Webb 1975).

9.3.2 - Respiration (including Metabolic Rate)

In order to further examine the metabolism of *Leedsichthys* via the model derived from BMNH P.10000, it is necessary to look at its respiratory constraints. The efficiency of respiration is a strong indicator of the metabolism of an animal, with metabolic rate strongly dependent on oxygen supply (Schmidt-Nielsen 1984). As noted by Pauly, the ability to efficiently process oxygen constrains growth (1994b, 1994c, 1994d) (as has been noted for other extinct animals, e.g. Sander & Klein 2005), and is closely related to gill surface area, asymptotic weight, annual food consumption and (more contentiously) aspect ratio of the caudal fin. Although metabolic rate can be scaled (a reading of around 2-10 calories per hour can be taken for a fish, whether homeotherm or poikilotherm, of the etsimated mass of BMNH P.10000; Schmidt-Nielsen 1984), this is not without problems, particularly as *Leedsichthys* lies at the outer limits of some graphs (Wilkie 1977), and frequently significantly beyond them (Hughes 1977).

This problem is also noticeable in attempting to scale the gill surface area from the estimated mass. The gill lamellae of bony fish have a complex structure (which, despite there being no obvious embryological relationship between them, bears a striking resemblance to the gill rakers of *Leedsichthys*, both in terms of the offset mesh and in transverse section, Hughes 1984; Lindsey 1988; Randall & Daxboeck 1984) with an efficient arrangement of blood vessels for gas exchange (Laurent 1984), but surface area has been recorded for a number of species (e.g. $9m^2$ for a 20kg sea bass *Dicentrarchus labrax*, Hildebrand & Goslow 2001), and workers have even generated power formulae for calculating numbers of gill lamellae and their lengths (e.g. for the ray *Torpedo*, Hughes 1984). Hughes (1984) noted that the slopes for the three characteristics of gill lamellae (numbers per unit length, average area and filament length) added together to produce the same slope as that of gill surface area against body mass. Although it is likely that *Leedsichthys* fits into the category of a large fish (*sensu* Moreau 1987) and therefore is likely to have an exponent relationship close to 0.9, this is an exponent that also accords with the tuna, which differs from all other fish in having a larger respiratory surface area than mammals (Randall & Daxboeck 1984), therefore is not a safe model to use. The extremely disparate range of constants deduced as exponents in extant fish families in order to apply a power formula calculation makes it difficult to estimate gill surface area with any confidence (Hughes 1984). However, Schmidt-Nielsen (1984) provides a useful compilation of data for several species of fish at masses approaching 100kg. Extrapolating from this graph, a crude estimate will produce a value of around $500\text{-}700m^2$ for the gill surface area. When one notes that Matthews & Parker (1950) recorded the gill surface area

of a 7 metre long basking shark (*Cetorhinus maximus*) as 270m^2, this does not seem an unreasonable estimated range for *Leedsichthys*, particularly given that relative gill area is greater in active fish as the surface area of the gills is related to oxygen consumption (Schmidt-Nielsen 1984), and the basking shark has traditionally been regarded as relatively inactive compared to other sharks (Matthews & Parker 1950).

Pauly (1994c) has argued that there is a strong link between gill surface area, caudal fin aspect ratio and growth performance index. If this was the case, then a fish with the aspect ratio of *Leedsichthys* BMNH P.10000 (4.32) should have a gill area index (which is a measure of gill area in cm^2 for a theoretical 1g of the fish in question) between 22.1 and 27.5. Taking an intermediate figure of 25 for the sake of argument, this would mean 25 x 7,000,000 = 17500m^2 gill surface area, different from the extrapolated reading by a factor of about 30. This figure may seem exceptionally far out from that suggested by the graph, but remembering that the respiratory surface per unit weight of fish can vary by a factor of ten according to the activity level of the species, the remaining factor of three easily lies within the error margin of the existing logarithmic plot.

As there are a range of measurements that can vary in differing ways to generate the same overall gill surface area for a given weight of fish of a particular activity level (e.g. thickness of lamellae, separation of lamellae, density of lamellae, filament length), there seems little point in trying to estimate or model these characteristics for *Leedsichthys* (Hughes 1966, 1972; Moyle & Cech 2000). The ways in which these characteristics interact are not yet fully understood for extant fish, and they can vary throughout a lifetime, even being subject to control by the fish in terms of the extent to which their gill lamellae are perfused with blood (Moyle & Cech 2000). Surface area is only one parameter that influences the uptake of oxygen, the others being the diffusion distance across the gill epithelia and the PO_2 gradient. Hughes (1977) presented three possible relationships between diffusing capacity (indicating maximum possible oxygen uptake) and body mass. The third category (his Fig. 4c) describes a negative relationship for the exponent relating body mass to metabolism and gill area. As this involves a strict upper limit of size, which *Leedsichthys* does not display, it seems that this must be dismissed as a possible model for this animal. The other two relationships described by Hughes involve either a static relationship between potential activity and size, or one in which the scope for activity increases as the animal grows. Although this latter scenario seems unlikely for a suspension-feeder, it cannot be entirely ruled out, as there might be an increasing need for improved ability to escape predation with increasing size. It may also involve the

increased potential for migration in order to avoid locally poor plankton conditions (Durbin 1979).

With increasing size not only do transport costs rise, so also do potential distances that can be migrated. This is important, as the ability to migrate large distances has been noted as a constraint on minimum size for a marine planktivore (Freedman & Noakes 2002). Peters (1983) presented formulae to generate figures for both cost of transport and potential migration distance which can be applied to *Leedsichthys*, if it is assumed that a quarter of its body mass is fat, and that it is a swimming homeotherm. For BMNH P.10000, the estimated transport cost under these conditions ($11W^{0.61}$) is 2437.3 Jm^{-1}, and the maximum nonstop migration distance ($0.9 \times 10^{6}W^{0.39}$) would be 28,433.5km. As the meridional and equatorial circumferences of the planet are both between 40,000km and 41,000km, this would mean that, assuming the conditions of these equations were fulfilled, this specimen of *Leedsichthys* would have had the potential to travel half the globe in one journey. This is without taking into account further potential ways of reducing total cost of transport, e.g. schooling (Weihs 1973, Webb 1975, Durbin 1979, Blake 1983, Lazzarro 1987, Webb & Gerstner 2000), which is energetically advantageous to groups of negatively buoyant fish and commonly occurs with other large suspension-feeders in today's oceans during migrations. Sims *et al.* noted that suspension-feeding whales migrated many thousands of kilometres for abundant patches of high productivity (1997). Eckert & Stewart (2001) suggested that whale sharks engaged in migrations that took several years to complete. Using ostracods as palaeogeographical markers, Whatley & Ballent (1994) noted substantial north-south and south-north faunal migrations via the Hispanic corridor (Tethys Seaway of Arratia 1996) between the European and South American marine realms during the Lower Jurassic (fig. 9.2A,B), with only north-south being evident in the Middle and Upper Jurassic, possibly related to a global cooling event (Dromart *et al.* 2003a,b). This may also indicate part of a likely migratory route for *Leedsichthys*.

The optimum velocities arrived at earlier may seem low for such a large animal, but for respiration to occur efficiently over the gill lamellae, the flow of water over them must be slow (Webb 1975). Freedman & Noakes (2002) pointed out that only the first 2-2.5mm of the capillaries in the gill filaments are involved in gas exchange. In order to maximise gas exchange, the flow must be kept slow, despite the fact that a large fish suspension-feeding as it moves through the water must be travelling at a relatively high speed, given the constraints on minimum velocity possible. However, the greater the volume of water across the gill lamellae, the more the boundary layer will be refreshed and the PO_2 gradient

maximised (Moyle & Cech 2000). Hoogenboezem *et al.* (1990) noted the widespread belief that flow over the gills was kept constant during suspension-feeding, but observed that this was not the case during X-ray monitoring of the suspension-feeding bream (*Abramis brama*). Cech & Massingill (1995) noted that in the Sacramento blackfish (*Orthodon microlepidotus*) a non-sieve based form of suspension-feeding allowed it to be independent of low oxygen concentrations and continue feeding by varying the deployment of its gill lamellae and increasing its gill ventilation rate. Although it is not uncommon for hypoxic conditions to result in selection for specialisations of gill morphology to tolerate such environments (e.g. Chapman & Liem 1995), it is unlikely that *Leedsichthys* would have had (or needed) such specialisations, as one would expect it to respire at the well-mixed water layer at the surface (Martin 1995) where the bulk of its planktonic prey would be found, at the top of the photic zone. Hypoxic conditions are rare in open oceans, although there is evidence that the Oxford Clay sea experienced periodic anoxic events (Hudson 2001), and given its significant body mass, *Leedsichthys* would have been particularly vulnerable to poorly mixed water.

9.3.3 - Nutrition

To review what *Leedsichthys* would have eaten, it is necessary to establish a likely niche for it. It has often been described as a filter feeder, although, strictly speaking, without proof that it is filtering the food from the inflow of the water by passing the water through structures that retain particles on the basis of size and shape, it should be referred to under the broader heading of suspension-feeder (Jorgensen 1966).

Smith Woodward's original description (1889b) states: "...it will be strange indeed if a monster with such powerful pectoral fins does not prove to have been possessed of a formidable dentition." In the ensuing years, no tooth-bearing bones have been recovered for this animal, and indeed out of some seventy specimens only two elements that might be jaw bones (one dentary and one maxilla) have been identified – Clark's statement (1998) of teeth-bearing jaws in the Hunterian's specimen of *Leedsichthys* was based on confusion with a specimen of *Ophthalmosaurus* (NDL Clark, pers. comm.). But what ecomorphological support do we have for the contention that this fish was a suspension-feeder, other than an apparent absence of toothed jaw elements, and elaborated gill rakers? Martill (1986a) was the first to attempt to answer the question 'what did *Leedsichthys* eat?', proposing a suspension-feeding lifestyle, arguing that 'needle-like teeth' on the gill rakers would probably have acted as a "filter bed for feeding on fine food such as plankton", and noting that "it would not be unusual to find a giant plankton feeder in a sea

rich in carnivores, as something at the bottom end of the food chain must have been in abundant supply." If this is the case, then it would mean that *Leedsichthys* was one of at least two Callovian lineages that appear to represent the first large (>1 metre standard length) planktivores to emerge in the world's oceans (see Chapter 5). The most specialised of the acanthodians (Long 1995), the Lower Permian *Acanthodes bronni*, which grew to a full adult standard length of significantly less than a metre (Frickhinger 1991) has been referred to as the first suspension-feeding fish using elaborated gill rakers (Miles 1973, Janvier 1996).

Diamond (1985) noted that the largest mammals and fish are all filter feeders, and McNeill Alexander (1998) also observed that large swimming animals tend to be suspension-feeders. There are a number of reasons why this should be the case. Matthews & Parker (1950), referring to the two largest sharks (the whale shark, *Rhincodon typus*, and basking shark, *Cetorhinus maximus*, both suspension-feeders), argued that the simple fact that the volume of a fish (and therefore the blood to be aerated) increases as a cube of its length whereas the surface area would increase as the square of the length, meant that development of a microphagous diet would be favoured with increasing size. Ware noted that, with increasing size, the metabolic cost of foraging and searching would increase faster than the energy gained, resulting in a decline in daily ration per unit of weight and instantaneous growth rate, which would be compensated for by adopting suspension-feeding, with reduction in energetic costs for prey searching and handling (1978). Webb & Gerstner (2000) noted a decline in strike success with increasing fish size, which tended to favour suspension-feeding. This was echoed by Batty & Domenici (2000) in terms of the increasing reaction distance of prey with increasing body depth and profile, which they underlined with a graph showing the relative profitability of biting and filtering over a range of prey density (Batty & Domenici 2000: Fig.2).

Morphology has been remarked on as a poor predictor of diet, with the noteworthy exception of midwater 'planktotrophic filter-feeders', for which a common suite of characters (including pointed pectoral fin, forked caudal fin, long closely-spaced gill rakers) has been highlighted (Motta *et al.* 1995), all features that *Leedsichthys* possessed. Characters regarding the gape, position of mouth, mouth area, and ratio of mouth area to buccal volume were also noted by Norton (1995) and Luczkovich *et al.* (1995), but given the already-noted paucity of jaw elements recovered for *Leedsichthys*, there is inadequate anatomical information currently available on this area of *Leedsichthys* skeleton for such evaluations to be made. Similarly, Sanderson & Wassersug (1990) indicated that a skull

length that constitutes between 25 and 28% of the Standard Length is characteristic in large ram suspension-feeders (baleen whales and the basking and whale sharks), and this proportion is also currently not determinable for *Leedsichthys*.

Sanderson & Wassersug (1993) provided a summary of morphological and ecological features common to both extant and extinct vertebrate suspension feeders, but at the time were unaware of *Leedsichthys* and so did not include it in their review (pers. comm. Sanderson 2001). They noted that for all vertebrate suspension-feeders (with the exception of the pterosaur *Pterodaustro*) teeth were reduced or absent, and that for large aquatic vertebrates swimming at high Reynolds numbers, continuous ram feeding was the common mechanism utilised (with the exception of the 4.5 metre long megamouth shark which is an intermittent suction feeder) (Sanderson & Wassersug 1993). In contrast to other large aquatic vertebrates, however, the megamouth shark frequents nutrient-poor deeper waters (Diamond 1985, Nelson *et al.* 1997), is a slower (Eckert & Stewart 2001), weaker and less active swimmer than other aquatic vertebrates (including *Leedsichthys*, judging from the figures presented in section 9.3.1.2), and possibly a less efficient filter feeder (Taylor *et al.* 1983). Its maximum size recorded so far is certainly significantly lower than for the basking and whale sharks (Compagno 2001).

Sanderson & Wassersug (1993) classified vertebrate suspension-feeders under four different headings: continuous ram feeders (e.g. basking shark, menhaden), intermittent ram feeders (e.g. rorqual whales), continuous suction feeders (e.g. tadpoles, mallards), and intermittent suction feeders (e.g.megamouth shark, cyprinid fish). We have no information on the ability of *Leedsichthys* to contract its muscles in order to expel water from its buccal chamber, but as Werth (2004) notes for the filter-feeding activity of the bowhead whale, during forward motion of an animal so large, the velocity changes outwith the head create (through the Bernouilli effect) a pressure gradient, with water entering the mouth at a point of high pressure, and exiting posterior to the gills at a lower pressure. This would obviate the need for such muscular contractions. Furthermore, the indications given for width of gape and buccal volume by the dimensions of the *Leedsichthys* gill basket specimen BMNH P.10156 (see Chapter 5) would seem to strongly argue that this animal was a ram feeder rather than a suction feeder (Norton 1995), and the elaboration of the gill rakers throughout the gill basket would further seem to confirm that *Leedsichthys* continuously ram fed on small nonevasive prey (Sanderson & Wassersug 1993).

9.3.3.1 - Biological Sieves:

Biological filters have long been recognised in suspension-feeders (Alder & Hancock 1851), with extensive reviews existing in the literature, primarily dealing with invertebrates (Jørgensen 1966, 1975). Mucous plays an important role in the mechanisms of many, if not most, suspension feeders. Potentially it is derived from oral cleansing mechanisms, but regardless of its source it is a highly viscous elastic gel, that can form fine elastic fibres as well as sheets, sometimes even observed to contain a true secondary structure of holes resembling the pores in a sieve (Jørgensen 1966). Mucous will spread over particles that come into contact with it, unless they possess a lipoid surface. It has been reported that mucous filters can even retain dissolved colloids from the water that passes over them (Jørgensen 1966). The properties of mucous come from mucoproteins and mucopolysaccharides that are highly effective at binding water and solutes. There is often less than 1% of these mucins present in the gel, but the mucin fibres form an internal reticular structure (or lattice) that can adsorb particles. Mucous agglutination occurs by acidification, the particles then being included within the lattice (Jørgensen 1966). Shimeta & Jumars regard mucous as a distinct mechanism of particle retention in its own right, referring to 'sieving' as a discrete mechanism unaided by mucous (1991). Rubenstein & Koehl (1977) note that as a filtration mechanism, 'sieving' suffers from high clogging and concommitant excessively high resistance to flow through the mesh, although this is usually immediately preceded by a large increase in collection intensity and can be regulated by the animal cleaning the filter (Shimeta & Jumars 1991). This means that animals can change the size of particles that they are feeding on by altering the frequency with which they clean their filter (Rubenstein & Koehl 1977).

Suspension-feeding is a form of biological hydrosol filtration (Shimeta & Jumars 1991). Suspension-feeders are typically non-selective in collection of particles (although selectivity usually arises prior to actual ingestion), clearing the surrounding water of particles at rates that are independent of concentration below certain levels and do not discriminate on the basis of their value as food. Suspension-feeding can be effected by passing water through structures that act as porous media to separate particles from fluid on the basis of their size or shape ('filtration') or by passing water along surfaces that are capable of retaining particles that come into contact with them (e.g. by secreting mucous). Within filtration, sieving is only one mechanism that operates, and is characterised by removing all of the particles larger than the pore size (a further upper size limit can also be set by screening structures (Jørgensen 1966)), and none of the particles that are smaller (Rubenstein & Koehl 1977). In addition to sieving, five further mechanisms are recognised for filters: direct interception, inertial impaction, gravitational deposition,

diffusive/motile particle deposition and 'scan and trap' (isolation of a packet of water containing a particle) (LaBarbera 1984). This last mechanism does not operate within vertebrate suspension-feeders, so will not be dealt with further.

For any suspension-feeder, feeding consists of four stages: encounter (transportation of the fluid containing particles past the suspension feeding structures or collectors); retention (capture and separation of particles from the fluid medium); transportation (of the particles to the opening of the gastrointestinal system); ingestion (LaBarbera 1984). Any filtration system involves three components: dispersed particles, a fluid medium, and a filter (either fibre or pore) (Rubenstein & Koehl 1977). These two elements of a filter, the fibre and the pore, respond differently to changing particle parameters, and differentially capture particles of different sizes. In a given encounter event, the retention probabilities will vary for each mechanism (Shimeta & Jumars 1991). The fibre can apprehend particles by sieving, direct interception (increasing retention with increasing size of particle), inertial impaction (increasing retention with increasing size of particle or velocity), diffusive/motile particle deposition (increasing retention with decreasing velocity of particle and decreasing viscosity of fluid), gravitational deposition (increasing retention with increasing size of particle and decreasing velocity). (There is also a suggestion that freshwater filtration may also involve electrostatic attraction, but this is not relevant to the marine animal under consideration.) The pore can apprehend particles through sieving, direct interception (increasing retention with increasing size of particle and reduction of pore size), inertial impaction (increasing retention with increasing size of particle or velocity, increasing relative particle density, reduction of pore diameter and changes of direction), diffusive/motile particle deposition (increasing retention with decreasing velocity of particle, elongation of pore and decreasing pore diameter), gravitational deposition (increasing retention with increasing size of particle and decreasing velocity, elongation of pore and reduction in pore diameter) (Rubenstein & Koehl 1977). In different scenarios, different mechanisms will become dominant for particle retention.

Scenarios will vary according to velocity, particle size and the nature of the filter. Silvester (1983) stated that diffusive/motile particle deposition was not a significant capture mechanism even with a fine filter, except for particles less than around 0.3 microns in size. In low relative water speeds, direct interceptions would be more significant, and at high relative water speeds with larger meshes, inertial impaction would be more important. Silvester went on to suggest that coarser nets were adapted for the efficient capture of large particles, and finer nets for smaller particles, but that this could easily be changed by

altering the adhesive properties of the mesh (1983). Rubenstein & Koehl (1977) stated that inertial impaction was only an important mechanism for organisms feeding at high velocities on large or dense prey, and that diffusive/motile particle deposition and gravitational deposition were only important mechanisms for organisms feeding at low velocities.

What is most likely to have been the dominant mechanism utilised by *Leedsichthys* to extract and retain particles from the water flowing through its buccal cavity? Gerking (1994) criticised the simplistic model of the mechanical sieve that was commonly used to explain filtration in fish, and argued for mucous entrapment as a more likely mechanism. The exact mechanics of the filtration process is unknown for most fish: for 70 fish species in 21 families in 12 orders that suspension feed (Cheer *et al.* 2001), Sanderson *et al.* (1996b) noted that there were 56 suspension-feeding fish species in 16 families for which the particle retention mechanism was unknown. Some suspension feeders can suspension feed on small particles without well-developed gill rakers (e.g. *Tilapia melanotheron* feeding on 50-100 micron particles, Hyatt 1979), and others are entirely unaffected in their ability to suspension feed when their gill rakers are surgically removed (e.g. *Sarotherodon galilaeus* tilapia, Sanderson *et al.* 1996b). For those fish for whom the process of trapping and extracting suspended food particles from the water for ingestion has been determined, the mechanisms vary widely (Gerking 1994). A functional continuum exists from pure sieving (Bemis *et al.* 1997), through crossflow filtration (Brainerd 2001), to trapping and extraction solely through the use of mucus (Goodrich *et al.* 2000). Throughout these mechanisms, the role of the gill raker in suspension-feeding varies from merely directing water flow (either towards the roof of the mouth, Sanderson *et al.* 1991, or towards the main current flow through the oral cavity, Sanderson *et al.* 1996a, to sieving particles, Sanderson *et al.* 1998, and acting as a crossflow surface, Sanderson *et al.* 2001). Even when dealing with two species of the same genus (*Oreochromis*) making similar oral movements at similar frequencies, different viscosities and locations of mucous can affect whether or not the gill raker elements are acting as sieves or sticky filters (Goodrich *et al.* 2000).

It is also worth noting, that although a suspension-feeding vertebrate might be specialised for a particular planktonic grade of prey, this does not mean that they will not take larger prey either opportunistically (Hain *et al.* 1981) or when "incidentally (nonselectively) inhaled" (Wright *et al.* 1983, Taylor *et al.* 1983). Traces of small fish vertebrae in the edentulous (and likely to be suspension-feeding) *Asthenocormus* from the Tithonian

Solnhofen limestone of Bavaria, and amongst the gill basket remains of a specimen of *Leedsichthys* (PETMG F174) under excavation (pers. obs.) and Taxon 13 (see Chapter 5) may well indicate the same phenomenon amongst these pachycormids. At the other end of the size spectrum, Sanderson *et al.* (1998) noted that incidental retention of small particles occurs on the gill basket of non suspension-feeding fish during respiration and particulate feeding, possibly due to charge or surface texture of the particles.

9.3.3.2 - Defining A Model For *Leedsichthys* Filtration:

In terms of how the buccal cavity of *Leedsichthys* was constructed, there is very little information beyond what can be deduced from the gill basket specimen BMNH P.10156, which principally consists of the ventral part of the branchial skeleton (the lower arches *sensu* Yasuda 1960) and a single hyomandibula. The main skull roof bones (parietal and post-parietal) have been identified in another specimen, and the maxilla, dentary and parasphenoid from a further three specimens. Lacking either a significant part of the skull of one individual, or even a series of elements from different individuals, is a major obstacle to understanding how the skull of this animal functioned during feeding. Reconstruction of likely flow patterns within the skull is severely constrained without knowing the length of jaw elements and the height of the skull that would go with the ventral gill arches. This makes it impossible to accurately model flow velocity change (and concomitant Reynolds number change) from the entrance of the mouth to contact with the gill rakers (Sanderson *et al.* 1994). Liem (1993) described seven patterns of transformation of the jaw elements in a trend from suction-feeding to biting in the teleostean skull, and the reversal of those trends could have been looked for with more skull material, but this is not possible with the specimens that have so far been recovered. Although there are of course problems with inferring function from form (Lauder 1995), a more complete knowledge of the shape of the buccal cavity would also have helped in determination of the jaw opening abilities of this animal (Lauder & Shaffer 1993).

Given that epibranchial organs (Howes 1981) occur in virtually all of the seventy fish species reported to suspension feed (Cheer *et al.* 2001), across four orders of 'lower teleosts' (Nelson 1967), it would be natural to seek signs on the epibranchial elements of modifications consistent with the presence of such structures in pachycormids, as this group was part of the initial teleost radiation (Arratia 1996). But the upper or dorsal branchial arch elements that have been recovered are severely fragmented, and so as much as it might be an expected structure for the extraction and compaction of smaller

planktonic elements (Friedland 1985, Jobling 1995), there is no evidence to support the contention that *Leedsichthys* possessed epibranchial organs.

Similarly, the presence or absence of gill raker cushions (van den Berg *et al.* 1994b, 1994c) as a thick padding of soft tissue on the branchial arches may be speculated on, given the ease with which the gill rakers seem to separate from the gill arches on death, but no evidence exists to substantiate this.

However, it is possible to establish a model for *Leedsichthys* filtration, based on BMNH P.10156 and the size and velocity estimates already obtained, with the following assumptions:

1) Although only the lower arch elements are present in BMNH P.10156, most gill rakers in bony fish are located on the ceratobranchials (Helfman *et al.* 1997), so it can be assumed that the main site of filtration in *Leedsichthys* was the ceratobranchial array. There are certainly no traces of gill rakers on the hypobranchials in this or any other specimen of *Leedsichthys*.

2) BMNH P.10156 is predominantly set in a concretion, so not much preparatory work has been done to the specimen. As such, although the gill rakers are often relatively undisturbed in relation to their presumed *in vivo* location on the ceratobranchials, they are infrequently visible throughout the concretion. This means that neither a detailed count of the gill rakers on each arch, nor a calculation of mean gill raker thickness and length is possible, as required by recognised formulae for calculating gill raker surface area (King & Macleod 1976, Gibson 1988), although these formulae have been referred to as unreliable to use for gill rakers with complex surface structures such as ridges or needles (Lazzaro 1987, Villalobos & Rodríguez-Sánchez 2002).

3) Although several mechanisms have been referred to as means of filtration by a variety of workers, it is noted that sieving is the dominant filtration mechanism, and Shimeta & Jumars specifically note: "the filters of baleen whales and large suspension-feeding fishes probably retain particles exclusively by sieving" as in high velocity environments the drag forces affecting "encountered particles greatly exceed the adhesive force of mucous" (1991) leaving sieving as the only likely effective retention mechanism. Therefore sieving will be regarded as the filtration mechanism that was used by *Leedsichthys*.

4) In the situation where sieving is the only mechanism, the calculation of filtration rates becomes significantly simpler. The particle encounter rate is simply equal to the velocity of the filtration surface multiplied by the product of the total area of the sieve and the particle concentration (Shimeta & Jumars 1991). The filtration area between the branchial arches was compared to an estimate of the cumulative gill raker filtration area, based on averaging the short distances of branchial arch where the proximal ends of gill rakers were still visible in what appeared to be an *in vivo* relationship. The interarch area for the gill basket BMNH P.10156 was calculated to be 319,709.775 mm^2, and the cumulative gill raker area was estimated to be 337,680mm^2. As this produces a difference of only 5.32-5.62% between the two figures, it was felt that the interarch area was a satisfactory approximation of the filtration area of *Leedsichthys*. Given Matthews & Parker's assertion of between 1,000 and 1,300 gill rakers per arch of a 9 metre basking shark (1950), it would be effectively impossible to excavate the gill rakers of BMNH P.10156 to mimic such a count without destroying the specimen. However, the large quantity of gill rakers collected from the field during the excavation of 'Ariston' (PETMG F.174) from the Star Pit (see Appendix VII/Liston 2006) offers a more quantifiable long-term approach to calculating actual gill raker area and gill raker variation than BMNH P.10156 can.

5) Given assumption 4, it is not necessary to have a complete gill basket for BMNH P.10000, in order to estimate its filtration surface. Although BMNH P.10156 consists of eight virtually complete ceratobranchials and some hypobranchials in a lifelike articulation, BMNH P.11823 has nine non-hypobranchial elements, consisting of epibranchials and ceratobranchials. The ratio between the longest ceratobranchial (III) and the first epibranchial gives us a mathematical relationship between them that can be applied to the first epibranchials of BMNH P.10000, in order to produce an estimate of the length of its third ceratobranchial. This length estimate can then be used to rescale the plan of BMNH P.10156 to produce an estimate of the filtration area of BMNH P.10000: 287,673mm^2. Although this scaling will not be affected by allometric growth rates between the gill basket elements and the standard length of the animal, the ratio between ceratobranchial III and epibranchial I established in the smaller (and presumably younger) individual BMNH P.11823 might be subject to allometric variation. The dataset however does not provide alternative resolutions to this problem, so the relationship between these two branchial elements will be taken as static at both Standard Lengths of this animal. When compared with the filtration area

of a 7 metre basking shark (0.5m²) (Sanderson & Wassersug 1993), the figure of 0.29m^2 for an 8.9 metre *Leedsichthys* seems low, but not unreasonably so.

6) There are three specimens of *Leedsichthys* that feature gill rakers in an *in vivo* position. In addition to BMNH P.10156, there is the small skull PETMG F34 and the branchial section of the Antofagasta specimen (I8-021173). Although there is a question regarding whether PETMG F34 is *Leedsichthys* or another taxon, primarily because of its anomalous gill raker morphology in possessing central needles rather than lateral ridges (see Chapter 6), it is interesting to note that the thin needles in PETMG F34 and the thick oblique ridges in BMNH P.10156 define the same size of laterally-orientated gap between them, of around 1.4mm. This suggests that, regardless of their relatedness or otherwise, both of these individuals were adapted as specialised feeders on a very similar grade of food supply, maintaining a similar pore size albeit with different thicknesses of fibres constituting the mesh of their filtration surface. This is a first sieve-like structure from which a measure of the size of material that can be sieved from the water column by this animal can be derived.

7) A second measure of mesh size is the gap between the gill rakers (Magnuson & Heitz 1971). Although the gap between gill rakers on the same branchial arch is identical for both PETMG F34 and BMNH P.10156 (4.5mm), the gill rakers from adjacent gill arches interdigitate, leaving the effective gap as 2mm and 3mm respectively. This is of interest for ecological interpretations of implied benthic feeding (Van den Berg *et al* 1993, 1994b), which will be discussed later.

8) A third possible 'mesh' structure has been determined in some Callovian and Oxfordian gill rakers – that of a suprafanuncular mesh that appears to sit as a superior continuation of lateral oblique ridges of the gill rakers, forming a laterally extensive honeycomb that appears to connect adjacent gill rakers together (see Chapter 6). Although the detailed structure of this mesh has proved difficult to elucidate, a measure of its pore size will be used in addition to the separation between the gill rakers and between the oblique ridges, in order to assess the likely extraction efficiency of this 'sieve'.

9) With *Leedsichthys*, only particle encounter can be modelled, with particle capture theorised and particle ingestion assumed. Although coprolites have been recovered from the Oxford Clay (e.g. GLAHM V3368), none have been identified as likely to

have been produced by *Leedsichthys*, so gut content information is lacking for this animal. Conversely, evidence of gastrointestinal tract contents in a non-selective suspension-feeder is not highly regarded as indicative of food choice, as some elements remain unaltered after passage through the tract, and others can disintegrate to unrecognisable detritus (e.g. naked flagellates and other delicate phytoplankton) without being ingested as food (Jørgensen 1966).

9.3.3.3 - Probable Food Of *Leedsichthys*.

A large obstacle to effectively modelling the sieving efficiency of *Leedsichthys* is the paucity of knowledge regarding the fossil record of plankton in general, and Mesozoic crustaceans in particular. Freedman & Noakes (2002) link the appearance of copepods in the fossil record with the explosion of teleosts, and indeed such a trend towards specialisation on a microphagous diet might well have applied to the contemporaneous appearance of the pachycormids, but our knowledge of the specifics of this pattern is very sparse. As noted by Cressey & Patterson (1973), although a Palaeozoic origin is implied for copepods, the only fossil evidence earlier than the Miocene comes from a non free-swimming parasitic form in the branchial basket of an early Cretaceous fish. Cressey & Patterson suggested that the lack of a fossil record for the free-swimming planktonic form might be due to this type being more poorly sclerotised, and therefore having a poorer preservation potential (1973). Pitt & Thomas (1969) speculated on a possible link between the high organic carbon levels of the Oxford Clay around Peterborough and the failure of Bryozoa to preserve. Hudson & Martill (1991) noted organic carbon content of the Lower Oxford Clay as between 2.1 and 10.4%, with a mean of 5.1%, Kenig *et al.* (1994) finding figures between 3 and 16.6%, and recent anecdotal findings as high as 14% (S. Gabbott pers. comm. 11/2002), with the bulk of the organic matter coming from high primary productivity from phytoplankton, based on primarily terrestrial nutrients. Although there is no direct means of converting this percentage figure into an annual measure of productivity similar to contemporary data (only a fraction of the carbon fixed escapes recycling in the surface waters and reaches the seafloor, J. Hudson pers. comm. 15/6/2006), it is clear that there are many indications of high primary productivity in this marine environment compared to today's levels, without specific details as to the character of this productivity. Although primary productivity directly reflects phytoplankton rather than the larger zooplankton that *Leedsichthys* is likely to have fed on, zooplankton grazers can be assumed to be present in significant proportions where phytoplankton are present in high numbers, forming the equivalent of around a tenth of the carbon mass produced by the phytoplankton (Ryther 1969).

Jørgensen, in his landmark review of suspension-feeding (1966), noted that as the relationship between water transport and the structure and size of the feeding organs must be phylogenetically fixed, so "food conditions similar to the present day must have existed for long periods of time." This allows a certain latitude in terms of superimposing aspects of today's plankton profile on to the Middle Jurassic, in order to provide a fauna for the modelled BMNH P.10000 to 'retrospectively' graze on.

Potential nutrient sources in the oceans consist of particulate organic matter, dissolved (or colloidal) organic matter, phytoplankton and heterotrophic organisms (e.g. bacteria, fungi, yeasts, heterotrophic flagellates, zooplankton). The relative proportions of these components varies according to geographical region and water depth by as much as two orders of magnitude in contemporary oceans (Ryther 1969), but peaks in primary productivity recur in predictable locations such as coastal and upwelling zones, particularly on the western seaboard of large continental masses (Jørgensen 1966).

It is interesting to note that the appearance of the first large suspension-feeding fish is coincidental with the opening of the gap between North and South America (fig. 9.2a, see also Figure 7a-c of Rees *et al.* 2000, Abb. 2 of Hungerbühler 1995 and Maps 23 and 24 of Smith *et al.* 1994), creating a global circum-equatorial channel. It is possible (though merely speculation) that the existence of such a channel might have strengthened the gyres responsible for increasing biological productivity in western continental coastal regions, creating a higher density of zooplankton in these areas than had previously been available, and thus favouring the development of a large suspension-feeder.

Large suspension-feeding vertebrates have been observed to migrate between regions of high productivity (Hain *et al.* 1981, Sims *et al.* 1997). As there is evidence of high productivity and associated increase in maximum size of various animals in the Middle-Upper Jurassic (Benton 1986), with water temperatures for the Peterborough Oxford Clay ranging from 20-29 degrees centigrade and 15 degrees for bottom waters (Anderson *et al.* 1994) it is conservative to assume that marine productivity maxima from today's oceans would be within the range of productivities that *Leedsichthys* would have fed on. As such, modelling a primary productivity profile for a Middle Jurassic grazing environment for *Leedsichthys* based on the Peruvian/Chilean upwelling zone, with around 300g/m^2 (Jørgensen 1966) or 155 x 10^6 metric tons (King & Macleod 1976) per annum, with peaks of 11.2g/m^2 per day (Ryther 1969), seems reasonable. This geographical region is

particularly suitable to use as a model, given that the Andes had reached altitudes of 1,000-2,000 metres by the Middle-Upper Jurassic (Rees *et al.* 2000), so the profile westward from the peaks to the edge of the continental shelf and the upwelling zone (the environment that the Atacama Desert *Leedsichthys* individuals would have inhabited, and the Peterborough individuals conceivably might have migrated to) would have been broadly similar to today's profile.

9.3.3.4 - *Leedsichthys* As A Sieving Suspension-Feeder.

Measurements were taken from specimens PETMG F34 and BMNH P.10000 to determine the relative significance of the pore and fibre components of the gill raker as part of a sieve, as these two filtering elements will differentially capture particles of different sizes (Rubinstein & Koehl 1977). The width of the pores in both cases was 1.4mm, but the fibre thickness was 0.4mm for PETMG F.34's *acus fanunculorum* and 0.7mm wide for the oblique ridges (Smith Woodward 1889b) of BMNH P.10000.

Measurements were then taken of the suprafanuncular mesh represented in Chilean specimens of gill rakers (see Chapter 6, fig. 6.24), to determine the maximum dimension of the honeycomb, to ascertain the largest objects that could pass through it. The figures for the honeycomb ranged between 4.8mm by 1.9mm to 4.8mm by 2.1mm, significantly larger than the pore and fibre dimensions for the gill rakers *sensu stricto*.

In comparison with the two figures for interraker gap for BMNH P.10156 and PETMG F.34 of 3.0 and 2.0mm respectively, it is clear that the filtering elements with the potential for extracting the most organic material from the water are the gaps between ridges (or *acii*) on the gill rakers.

These measurements were then compared with figures for densities of plankton and different grades within samples of plankton from the Atlantic (de Ciochomski 1967, June & Carlson 1971). Although it was hoped that relevant data could be obtained for the Peru/Chile upwelling region, the necessary data for the densities of different size grades of plankton for this geographical region were not available, although SAHFOS (Sir Alister Hardy Foundation for Ocean Science) have plans to collect this data in the near future (D. Johns, pers. comm 20/6/2006). As such, this means that actual percentages of plankton and other nutrients representing a broadly biologically similar environment to *Leedsichthys* cannot yet be directly compared to the sieve potential calculated for this animal. However, comparison with Atlantic plankton data does give a coarse pattern of the relative

efficiencies of nutrient extraction for *Leedsichthys*, in terms of what types of food this animal is likely to have been able to extract, as gill raker sieve parameters do tend to covary with the zooplankton available (Hjelm & Johansson 2003).

A sieve with a pore-size of 1.4mm would extract around 38% of the volume of zooplankton from the table presented by June & Carlson (1971). In comparison, if the pore-size of the sieve employed was increased to 2.0mm, the net percentage haul by volume goes down to <2.4%. In terms of planktonic organisms that have mean dimensions large enough to be caught in the pores without relying on a particular orientation for them to be intercepted by the gill rakers, the vast bulk in both scenarios consists of copepods (with the added possibility of large diatoms e.g. *Triceratium* spp., de Ciochomski 1967). Given that whale sharks have been observed actively feeding in waters at the level of the Tropic of Cancer on the western seaboard of Mexico coastal upwelling zone where more than 90% of the copepods present were >1.5mm *Acartia*, it is not surprising that this would be a pore-size selected for by a Middle-Upper Jurassic suspension-feeding equivalent (Clark & Nelson 1997). As noted before, Freedman & Noakes (2002) pointed out that the appearance of copepods in the fossil record is close to the explosion of the teleosts (but see also Cressey & Patterson 1973 re implied earlier age of the lineage).

Although these figures cannot be regarded as directly reflecting the planktonic profile of the Middle-Upper Jurassic, they do give an indication of the size grades that one might expect *Leedsichthys* to be specialised on, and in this regard 38% does seem a lower value than one would expect for a highly successful (given its estimated size) suspension-feeder with such a specialised ingestion apparatus. This may, of course, simply be because the planktonic data used are unrepresentative, perhaps because larger grades of zooplankton were present in greater abundance in the Callovian-Kimmeridgian than are present today. Shimeta & Jumars have pointed out that animals feeding at high particle flux with low filtration efficiency can survive well as long as particle capture rates are high (1991). The lower than expected value of 38% might also be because the buccal cavity dynamics in *Leedsichthys* allowed for the extraction of more material from the water passing through, by reducing the flow velocity and thus reducing the Reynolds number, and so increasing the encounter rates of the particles with the sieve structure. Incomplete knowledge regarding the relative sizes of a complete set of bones surrounding the buccal cavity make it difficult to assess whether *Leedsichthys* possessed a cylinder-shaped suspension-feeding cavity, or a more cone-shaped one (Liem 1993), that would have had the effect of significantly reducing internal flow velocity. Bearing in mind the potential for variation of

skull components associated with specialist feeding (e.g. Winemiller *et al.* 1995), it is thought to be unwise to speculate in this regard.

It is worth noting that several authors have drawn attention to the degree of flow resistance generated by the gill filaments (Hughes 1972, Webb 1975, Magnuson 1978, Lazzarro 1987), Webb commenting that around 10% of a fish's theoretical drag comes from gill resistance. Similarly, the filter in suspension-feeders will cause signifcant problems of hydrodynamic drag (Rubinstein & Koehl 1977) with Vogel observing that the finer the mesh of the filter, the greater the resistance to flow (1994). As such, mesh size must increasingly become a compromise dictated by the need to travel efficiently through the medium and the need to efficiently extract nutrients from that medium (Durbin 1979).

Shimeta & Jumars (1991) have argued that the direct interception rates of a filter increase linearly as a function of velocity in low Reynolds (or 'creep') flow, increasing non-linearly with an R_e around 1 (with streamline compression), and increasing even more sharply above 10 (due to vortex formation). This means that velocity variations have an increasing influence on encounter rates as the Reynolds values of the filter increase.

In *Leedsichthys*, although arguments can be made for using the gape of the mouth and the interbranchial gap, the primary collector area (*sensu* Shimeta & Jumars 1991) was the gill raker. The Reynolds values for these structures can be calculated using the derived figure for the optimum feeding velocity ($1.77ms^{-1}$), the height of the gill raker (0.007m) and the reciprocal of the kinematic viscosity for sea water. As the kinematic viscosity has not been calculated for the temperature ranges of 20-29 degrees, with salinity in the Oxford Clay sea being unknown, a calculated value for 15 degrees and 35% salinity was used instead (Videler 1993). Although this is unsatisfactory, it provided a value of 1.05×10^4 for the gill raker, which indicates the order of magnitude involved in this animal suspension-feeding. It is worth noting, however, that Cheer *et al.* (2001) noted that an individual fish can suspension feed over an Re range of almost two orders of magnitude during its lifetime.

The quantity of water that could be processed by BMNH P.10000 in an hour, would be equivalent to the product of its optimum feeding speed and its filtration area, which gives a figure of 1847.88 cubic metres per hour. A 7 metre basking shark was calculated by Matthews & Parker (1950) to filter 2215 cubic metres of sea water over the same period of time (Sanderson & Wassersug 1993). This can be viewed, in terms of clearance rates

(Jørgensen 1966), as taking just over ten years for this one specimen of *Leedsichthys* to filter the surface waters of the Peru/Chile coastal upwelling zone today, assuming a mouth gape equivalent to 12% of its body length, as per a whale shark of the same Standard Length (Gudger 1941).

Sanderson *et al.* (1994) assessed the flow velocity in paddlefish, and noted that the velocity of the water at the gill rakers had dropped to 60% of the velocity of the water entering the mouth, creating Reynolds values between 1 and 40. It is possible that other factors similarly existed to reduce the flow velocity in the buccal cavity of *Leedsichthys*, with the gill arches and the gill rakers forming a resistance to the flow (Hughes 1972), but this would be an effect that would develop as the flow travelled across the gill rakers, becoming slower as it travelled posteriorly within the buccal cavity. Also, it cannot currently be assessed to what degree specific positioning of the branchial arches and the gill rakers with regard to the flow direction would alter this situation. Rubenstein & Koehl (1977) noted that suspension feeders adopt behaviours which optimise the flow velocities for their filters, so that for the greatest efficiency the fibres of the filter would lie perpendicular to the direction of flow (Spielman & Goren 1968). Constant swimming speed (as observed for suspension-feeding menhaden, Durbin & Durbin 1975) is essential for filter efficiency, to prevent distension escapement leakage (Boyd 1976), and maintain optimum retention efficiency (Shimeta & Jumars 1991). There are other factors (e.g. satiation, control over filter cleaning, time spent feeding) that also may distort estimates of filtration efficiency over unit time (Shimeta & Jumars 1991).

9.3.3.5 - Other Suspension-Feeding Behaviour

The rate of water transport through the filter must at least be adequate to cover the nutritional requirements of the animal for at least part of the year (Jørgensen 1966). Suspension-feeders incidentally supplement their diet with 'non-selective' ingestion (Wright *et al.* 1983) of food that is not their primary source of nutrition. A good example of this form of incidental ingestion (or 'collateral damage') is the whale shark found to have ingested a tuna (Helfman *et al.* 1997). This is hardly the microphagic diet that this animal is adapted for, yet it was ingested nonetheless. Possible signs of this phenomenon were found in the form of isolated 4-5mm wide osteichthyan vertebrae during the excavation of the gill basket area of the Star Pit *Leedsichthys* (PETMG F.174, see Appendix VII/Liston 2006), and have been noted in specimens of Taxon 13 and *Asthenocormus* (see Chapter 5).

9.3.3.6 - Possible Iliophagy

Before reviewing the evidence for *Leedsichthys* being a facultative or opportunistic iliophage, it is worth examining some of the work done on other animals that feed on nutrient sources within sediments on the sea bottom.

There are many examples of fish that opportunistically become iliophagous. Ringler's (1979) review of benthic feeders observed that as distribution of fishes can change seasonally, so it can be expected that diets will change as well. Jobling (1995) refers to adult pleuronectids taking prey from the sediment by suction. Sokolov and Vasil'ev (1989) noted the benthic feeding habit of the sturgeon *Acipenser baeri*, with sediment on occasion making up 90% of the animal's stomach contents. Bowen's review of detritivory notes that both *Sarotherodon mossambicus* and *Mugil cephalus* sort sediment from prey in their oral cavity when bottom-feeding (1983). Lazzarro (1987) referred to the silver carp's ability to feed on bottom sediments in order to survive times of low plankton biomass. Janssen (1978) noted the advantage that the broader feeding repertoire of the coregonid cisco had over the alewife, in being able to switch to bottom-feeding. De Ciochomski (1967) specifically noted that the suspension-feeding *Engraulis* became iliophagous in winter. Non-fish also can be opportunistic in this way, with gray whales using intraoral suction to extract invertebrates from sediment on the Bering Shelf of Alaska (Hans Nelson & Johnson 1987, Hans Nelson *et al.* 1987, Werth 2004). Plesiosaurs have been reported to have done the same, through gut contents predominantly preserving the remains of epibenthos (McHenry *et al.* 2005).

In dealing with benthic feeding, Lauder (1983) noted that the decoupling of actions involved in obtaining prey allowed the development of different actions with which to obtain prey. He referred to *Lebiasina*, using its jaws and muscles to feed in a different way on bottom sediments, in comparison to the way that it used its jaws and muscles at the surface of the water, as an example of this broader feeding repertoire. Similarly, van den Berg *et al.* (1994b), regarded their reducible channel model (a form of interdigitation of gill rakers) as indicating a facultative rather than obligate suspension feeder, so that the secondary feeding option of selection of invertebrates from the substratum would be available to *Abramis brama*. Van den Berg *et al.* reasoned that the reducible channel permitted the interraker gap to be varied significantly enough that gill rakers would not be damaged by sediment particles when bottom-feeding (1994b).

As has been observed, *Leedsichthys* gill rakers interdigitate in this manner, and it can be seen that adjustment of the ceratobranchials relative to each other would allow them to move and vary the size of the gap for suspension-feeding. Geister (1998) mentioned feeding traces from the Lower Callovian (Dietl & Gygi 1998), which have been reviewed as possible traces of *Leedsichthys* feeding elsewhere (see Chapter 4). Van den Berg *et al.* (1992) has noted that because the energy ratio (equal to energy intake through food/energy consumption) is proportional to the filtering area divided by the mass of the fish to the power of 0.75-0.9, the energy ratio will decrease with increasing mass, so that filter feeding will become less suitable as the sole feeding mechanism. This suggests that rather than being simply a useful secondary option, diversification to other means of obtaining food beyond filtering from the water column might become a requirement after a certain critical mass is reached.

It is worth reflecting on the basking shark and the phenomenon of gill raker loss that has been reported periodically for them over winter (van Deinse & Adriani 1953). It has been noted that it is not a loss that appears to be universally experienced at the same time throughout a population of basking sharks. It is unknown what triggers this change, whether it is a decline in plankton intake or alteration of diel patterns due to daylight hours changing. Sims *et al* (1997) noted the idea that basking sharks might be able to utilise their livers as a nutrient store over winter if they hibernated. Sims later demonstrated that basking sharks did not hibernate (Sims *et al.* 2003), but probably spent the winter in deep water on the mesopelagic slope down to 2200 metres, where late stage calanoid copepods overwinter (Sims 1999, Sims *et al.* 2003). It seems unusual that they might be attempting to feed on this prey during the time that they might shed the gill rakers that are their principal means of extracting zooplankton from the water. The long streamlined gill rakers of basking sharks (fig. 6.5) are of a very different character to those of *Leedsichthys* (fig. 6.6), and it may be that losing them for a period over the winter allows them to become temporarily iliophagous without their gill rakers interfering with the efficient sorting of organic material from the sediment.

Current models of the Oxford Clay sea reflected by deposits around Peterborough are interpreted as traces of an epeiric sea, no deeper than 200 metres (epipelagic), with what would today be regarded as a tropical surface water temperature range of 20-29 degrees centigrade. Although the Chilean *Leedsichthys* material is found in a former upwelling zone, the Peterborough material is interpreted as receiving its nutrients from terrestrial sources (fig. 9.2b). In less than 200 metres water depth, a diversity of life would have

enriched the sediments, making them an excellent option for benthic feeding in times of restricted plankton growth. This would have also been the case at the Chilean upwelling zone, where a high level of biomass would be expected at the edge of the shelf, before the start of the continental slope. This range of environments matches closely to the littoral-tachypelagic ecomorphotypes used by Compagno (1990) to describe the habitats of both whale sharks and basking sharks. The absence of *Leedsichthys* remains from the Sundance Formation marine outcrops of North America has been commented on before (section 4.8) as an oddity when contrasted with the various northern European sites of similar age, but the Sundance Formation is interpreted as near-shore/shallow marine (Schaeffer & Patterson 1984, Uhlir *et al.* 1988) in a desert belt, and it may be that this was just too shallow a water-depth for *Leedsichthys*, in terms of its requirements for strong nutrient sources in environments where plankton could flourish (fig. 9.2b).

9.3.3.7 - Taphonomy and Predation

A full assessment of the taphonomy of *Leedsichthys* specimens would be premature at this time, as save for Ariston from Bed 14 of the Star Pit (see Appendix VII/Liston 2006) which is awaiting completion of its excavation and final preparation of elements, there are no specimens which have emerged that could enlarge on the thorough work done by Martill in his 1986 review of the preservation of fossil vertebrates in the Lower Oxford Clay (Martill 1986b). The only exception to this statement is the specimen from Wallücke in northern Germany (see Chapter 4) which is scattered through a variety of collections, inadequately prepared and largely difficult to discern from its matrix, so currently would add little to our knowledge, despite having a (retrospectively-compiled) site map (Probst & Windolf 1993, Michelis *et al* 1996). All other specimens (save for Atacama Desert material, which lacks any record of the distribution of its components in the field) are either partial fragments or were excavated by Alfred Leeds, who not only did not make site maps, but washed the bones clean from the matrix, making it impossible to reconstruct how they were found (BMNH P.10156 being a noteable exception). A full account of the taphonomy of *Leedsichthys* specimens will accompany the published description of PETMG F.174.

Assessing what preyed on *Leedsichthys* is not as easy to determine as with other taxa in the Oxford Clay sea. The fragility of the bones means that many of the bones are rarely intact enough to give signs of tooth or other predation marks, in sharp contrast to the remains of marine reptiles from the same formation (Anderson 2004). Of the roughly seventy known specimens of *Leedsichthys*, only one sub-adult and one juvenile can be identified, the rest

of the material appearing to come from individuals that seem to have reached the 8-12 metre range described elsewhere (see Chapter 7). These individuals represented a substantial quantity of protein. It is hard to imagine that *Leedsichthys* would not have been the subject of much predator attention, and yet only three specimens show possible traces of attack. There are certain advantages that it will have had over its likely marine reptile predators once it achieved adult size. Although it is not possible to determine what triggers might have been possible in such bony fish (Eaton & Hackett 1984), Domenici & Blake have noted that the incidence of low-performance fast-starts with a large turning angle increases with Standard Length in fishes (1997). Webb determined that turning radius was the product of 0.17 and Standard Length, which for BMNH P.10000 would mean a turning radius of around 1.5 metres (1976). The depth of *Leedsichthys*' body is likely to have been around 1.5-2.0 metres, given the height of its caudal fin (2.74m for BMNH P.10000), and such a deep body would have been an important factor, as it is likely to have deterred gape-limited predators (Domenici & Blake 1997), constraining areas of its body that could be attacked. It is unlikely that the body was much higher than this, as the 'Ariston' specimen (PETMG F.174) was recovered with pectoral fins in an *in vivo* position, agreeing with Martill's scheme for fish that preserved 'right way up' rather than on their sides when the span of their pectoral fins was greater than the height of their body (Martill 1986b). A deep body would also indicate an adaptation for the enhancement of thrusts (Domenici & Blake 1997). The large size of the tail and the likely flexibility of the body (for high amplitude propulsive movements) would also have been indicators of adaptation for acceleration rather than cruising, indeed the likely body flexibility would help to improve the performance of the animal's fast-starts, due to a lack of stiffness at its centre of mass in comparison with fully ossified fish axial skeletons (Domenici & Blake 1997, Batty & Domenici 2000). *Leedsichthys* would have physiological advantages over marine reptiles in terms of not having to come to the water surface for air. Although it is likely that, based on comparisons with other contemporary marine reptiles (S. Fielding pers. comm., M. A. Taylor pers. comm. 1/7/2005) and mammals (Liston 1988) such Jurassic equivalents might well have been able to stay submerged for hours rather than minutes, in reality, provided that *Leedsichthys* could survive the first attack and the subsequent period of pursuit dictated by the optimal foraging requirements of its attacker, it would probably only need to evade for a matter of minutes before the chase would have been broken off.

There are certainly indications of damage to the bones of *Leedsichthys* in various specimens, usually elongate fin-related elements, although it is a moot question whether they arose from the animal colliding with undersea obstacles instead of from an attack by

another marine denizen. Examples of these isolated breaks with subsequent callus growth occur in BMNH P.47412 and GLAHM V3363. Two specimens, however, suggest stronger evidence for attack rather than accidental breakage of elements. These feature a series of elements with marks that give an arc unlike one of impact, but strongly resembling the curve of a bite. The first specimen (BMNH P.6924) was excavated by Alfred Leeds and accessioned by the BM(NH) in 1893 (Liston & Noè 2004), and consists of a series of dorsal fin-rays (fig. 9.3A-C). Although, as was Alfred Leeds' usual practice, they have been washed clean of their clay and so do not have any matrix to indicate their precise relations when found, a comparable specimen excavated by Henry Keeping (CAMSM J.46873, fig. 2.3, fig. 4.10) has preserved some matrix that indicates that these elements were in contact at their broad bases. With this knowledge, the arrangement of the bones in life can be reconstructed, providing an estimated width of bite of 130mm, with signs of a tooth impression of 47mm diameter. As far as is known, a bite and tooth this size in the Oxford Clay sea could only have been made by a pliosaur, the plesiosaurs having too small a gape (Andrews 1910). A pliosaur tooth of this girth (probably *Liopleurodon*) would have a crown of around 100mm length, with a total length of around 300mm (L. Noè, pers. comm., 5/7/2006). The second specimen to give evidence of the specific mouth shape of an attacker is BMNH P.62054, a collection of fin-rays (probably pectoral, but this can only be confirmed or denied once the preparation of the pectoral fins of PETMG F.174 has been completed) donated by I. Crowson (via D.M. Martill) in July 1985 from the Bunting's Lane borrow pit near Peterborough, believed to be from Bed 12 (Hudson & Martill 1994). A section of this was figured by Martill (1986b: plate 9C), but viewing the entire specimen (fig. 9.3d) indicates the constrained arc of the damage, again suggesting a mouth. Smaller in size, it could be from a plesiosaur as well as a small pliosaur (Andrews 1913), but it is too broad and curved to have been made by a crocodilian.

Martill (1986b: plate 10) figured a skull element of PETMG F.1 with a *Metriorhynchus* sp. tooth embedded in it as an example of an unsuccessful attack by a crocodilian on *Leedsichthys*. Martill cited callus growth around the tooth as evidence that *Leedsichthys* evaded its attacker and lived long enough for bone regrowth to occur. Examining this element in detail, it is difficult to determine the presence of callus growth: the bone appears largely homogeneous over a wide area, with some thin traces of bone on only one side of the crocodilian tooth that appear to have been pushed up by the entry of the tooth into the bone (fig. 9.4). If there was true bone repair, as witnessed in other specimens of *Leedsichthys*, it would be expected that bone regrowth would be visible around all areas of

the entry wound generated by the tooth on the bone, and this does not appear to be the case. If this interpretation is correct, then the tooth may have become embedded either as part of a fatal attack (or one close to the eventual time of death, therefore showing no sign of bone regrowth) or during post-mortem scavenging. Identification of the bone in question as a right hyomandibula further casts doubt on such a wound being the result of an attack on a living animal. It is extremely hard to envisage how a marine reptile of any sort could bite into the hyomandibula of *Leedsichthys* without extensive - and terminal - initial damage to the skull being inflicted by the predator in order for it to have access to (and enough purchase on) that bone in order to embed one of its teeth in it. As such, it seems most likely that this embedding of the tooth results from post-mortem scavenging.

Other specimens exhibit indications of post-mortem scavenging. Wrapped with elements of BMNH P.6921 in 1888 newspaper was a tooth from *Pachymylus leedsi* (see GLAHM 132251), together with a coprolite/bromalite-like (McHenry *et al.* 2005) mass. This would seem to indicate that these elements were closely associated with the first remains of *Leedsichthys* to be excavated. Hybodont teeth have been noted imbedded in the pectoral fin fragment of BMNH P.10000 (see Chapter 7), and others have been seen at the bases of several dorsal fin-rays in a private collection from the Oxford Clay around Peterborough (pers. obs., July 2002).

9.3.4 - Irritability

Aspects of the nervous system are of course virtually impossible to determine for *Leedsichthys*. The mandibulary sensory canal of the dentary (fig. 8.63c) is the only neural pathway to have been determined with any confidence in any specimen of the animal. A full neurocranium has not been found from which an endocast could be taken, and the basiocciput and parasphenoids that might indicate a basal length of the brain come from different individuals. Although many workers have used such endocasts to calculate body mass (e.g. Hurlburt 1999, Wroe *et al.* 2003), methods have not yet been devised to work in reverse. The best guide is still Jerison's landmark 1973 work (cited in Schmidt-Nielsen 1977), which predicts (using the estimated mass of BMNH P.10000) a brain mass of around 100 grammes for a fish of the mass of BMNH P.10000 (Helfman *et al* 1997), but as it is outwith the zone defined within the logarithmic plot for fish brains, it is hard to assess if there is any value in such an estimation. Haller's Rule of brain/body allometry would generally indicate that relative brain size would decrease as body size increases (Roth *et al.* 1990).

Even if endocasts were possible for this animal to determine its brain capacity, this would not tell us about its 'intelligence' or neural processing ability: as has been demonstrated elsewhere, brain-size can be compensated for by increased connections for a given volume (Timson 1990). An endocast might, however, indicate the relative development of different areas of the brain: comparisons with the well-developed diencephalon and telencephalon of both *Acipenser* and *Amia* (Niewenhuys 1982) would make it seem reasonable that pachycormids might display similar development of different regions of the brain. The value of this would be a measure of the potential for a well-developed olfactory and gustatory sensory system, to aid in prey detection.

Lazzarro (1987) presented Holling's model for predation for suspension-feeders, but omitted the phases of 'detection' and 'approach' from the revised model. Although visual acuity in fish is variable (Van der Meer *et al.* 1995), Durbin (1979) pointed out that visual acuity tended to improve swiftly with increase in fish size. However, visual detection is of use to a suspension-feeder only in terms of navigation and detecting predators, and there will be mechanical limits on the maximum size of an eyeball that will constrain how far this trend will extend. In detecting its food, a suspension-feeder operates independently of light, often schooling with other planktivores to more efficiently explore larger volumes of water, and evidence exists that some at least can use chemoreception as a trigger (Lazzarro 1987) with many examples of fish in general displaying acute olfactory sensitivity (for a brief review see Tucker & Smith 1976). The sensory abilities of contemporary large suspension feeders are still poorly understood. Although Matthews & Parker (1950) dismissed the idea that basking sharks could detect their prey from distance, and believed that these animals utilised a purely random search pattern, recent work (Sims 2006) has demonstrated that basking sharks are able to detect food from distance far more efficiently than modelled random search patterns would predict. Basking shark fishermen (H. McCrindle, pers. comm. 2/11/2006) have noted behaviours of basking sharks that seem to indicate the ability to follow scents, and that their preferred food has an unusually strong smell.

Nevitt's work (1991) has led to interpretation of plankton-related olfactory landscapes both below and above (Nevitt *et al.* 1995, 2004) the water surface. The metabolic byproduct of dimethyl sulphoniopropionate (DMSP) in marine phytoplankton is Dimethyl Sulphide (DMS), which has been demonstrated to attract birds over large distances that feed on zooplankton, and could have similar carrying potential in the marine environment (Nevitt,

pers. comm. 2004). Lazzarro (1987) also suggested that zooplankton waste products could be a sensory trigger for planktivores.

It seems highly likely that *Leedsichthys* would have had a non-visual means of detecting its prey. There are some unusual means of chemoreception described for fish (Kotrschal 1995), but examples of more widespread means by which such biochemicals could be sensed are also recorded. Gerking (1994) mentions the phenomenon of fish 'gulping' water in order to taste it, and, contrary to Kyle (1926), Iwai (1963, 1964) demonstrated comparatively widespread occurrence of taste buds on the gill rakers of fish.

9.3.5 - Growth

Growth is the net organic production of an organism, a function of the food that it has assimilated, minus metabolic losses. Case made comparisons between different animals for growth rate, and calculated figures for rate of growth of fish based on their body mass (1978). Using his regression equation for fish produces a figure for the estimated increase in mass of BMNH P.10000 (7,000kg) of an average of 1.23 grammes per day for the period during its lifetime when growth would be expected to be constant, from roughly 10%-90% of its adult body size. This growth would have to be supported in addition to basal metabolism by the rate of ingestion of the animal, calculated at 5401 Watts for BMNH P.10000 ($10.7 \times mass^{0.703}$, Peters 1983). These figures could be utilised as markers by which to check how realistic any biological model based on suspension-feeding via the reconstructed gill basket was.

9.3.6 - Excretion

In bony fish, the gills are the main site of nitrogenous excretion, diffusing away as ammonia (Hildebrand & Goslow 2001), but there are waste products from the gut. Depending on the consistency, excreta from fish the size of an adult *Leedsichthys* could have a fair potential for survival. Coprolites occur regularly within the Oxford Clay (e.g. GLAHM V3368, a series collected by Alfred Leeds), but no study has yet been undertaken on them to examine their constitution and assess the possibility of being able to constrain likely producers of them. In this context, the bromalite/coprolite that is part of specimen BMNH P.6921 should be considered for future examination.

9.3.7 - Reproduction

Case (1978) argued that 'large' fish only achieved sexual maturity at two thirds of their final body length. Given the evident large size of specimens of *Leedsichthys*, it seems

highly unlikely that this animal would have adopted a semelparous strategy (one-off reproductive event during the lifetime of the animal), as this tends to be used by r-strategists, and large size is associated more closely with k-strategists (Peters 1983). This means that iteroparity is a far more reasonable assumption for a reproductive pattern for *Leedsichthys*. The larger a fish, the larger its ovaries, and the more eggs that it will produce (Helfman *et al.* 1997). Applying relations calculated for clutch, individual egg and maternal body mass to BMNH P.10000 results in an estimated clutch mass of around 100kg, consisting of roughly 10 gramme eggs (Peters 1983). In terms of two contemporary comparator animals, this places *Leedsichthys* between the periodic strategist the sunfish (*Mola mola*, the largest teleost, in terms of mass, producing 3.0×10^8 eggs of around 1mm diameter per clutch) and the whale shark (*Rhincodon typus*, the largest suspension-feeding fish, with a clutch of 300 young, making it the most periodic of the equilibrium strategist elasmobranchs) (Freedman & Noakes 2002). Lindsey (1975) noted that large fish within a given family tend to lay larger eggs, but no examples of eggs of pachycormids are known for comparison. Large size or specialist needs (Grimes & Turner 1999) tend to make an animal vulnerable to extinction (Musick 1999), but it is easier for large animals to survive local ecological problems (Bakker 1993), unless their specialist needs restricts the number of viable sites, for example, breeding waters, that are available to them. It is widely recognised that larger species invest less in their offspring (in comparison to their own body weight) per unit time (Reiss 1989). A dispersive planktonic larval stage is common to most marine fishes, regardless of the habit of the adult fishes, simply because of the periodic high productivity of zooplankton in the open ocean (Helfman *et al.* 1997), and therefore would be predicted for *Leedsichthys*.

Further work on the remains of biologically (rather than geologically) younger individuals, exhibiting more detail of the early years of growth, might lead to estimates of size at hatching/birth, which would indicate the applicability of the above calculations of clutch mass to the reproductive strategy of *Leedsichthys*, and enable estimates of likely population biomass to be made (Peters 1983).

9.4 - CONCLUSIONS AND FURTHER WORK

The palaebiology of *Leedsichthys* has been reviewed, with principal focus on locomotive ability and likely feeding behaviours. It is regarded as highly likely (due to size and skeletal details) that *Leedsichthys* was a suspension-feeder, and was probably able to facultatively feed on epibenthic invertebrates. Evidence of predation by pliosaurs and

scavenging on its remains by metriorhynchids and sharks (hybodonts and chimaerids) is presented.

Future work: Avenues for further work with regard to growth and coprolites have been outlined above. Work has begun to reconstruct the more detailed function of the gill basket of *Leedsichthys* in a technique similar to Sutton *et al.* (2004). The sources of information for this are three-fold: firstly, CT scans have been taken of an 85mm block of Atacama Desert gill raker material (fig. 9.5A-C), to enable the virtual reconstruction of the suprafanuncular mesh described earlier. Processing of the data by Robert Davey of Voxar (Barco N.V.) has already resulted in some initial processed images that have expanded understanding of the fine detail of this critical component of this animal (fig.9.6A-C).

This will be combined by the Digital Learning Foundation with images from sections of the same 85mm block of gill rakers cut with a Logitech diamond wire saw (fig. 9.6D), and scans of acetate peels (fig. 9.6E) taken over 3mm of the block for high resolution of one particular section, to produce a reconstruction of the relationships of a cluster of gill rakers. This can then be further expanded, by analysis of the many hundreds of gill rakers retrieved from the Star Pit dig, to create a model of variation in the gill raker morphology of a single individual of *Leedsichthys*. Combined with general information of branchial arch configuration of BMNH P.10156, a full digital reconstruction of the ventral gill basket of *Leedsichthys* with and without suprafanuncular mesh can then be virtually assembled to model effectiveness in extracting different particles from the water column, analyse particle activity under different flow regimes and compare with the gill raker arrangement displayed by PETMG F.34. The aim of this would be to examine if the structures in PETMG F.34 represent specialisation for a different feeding niche, and to study the function of the mesh in particular, to determine if its primary functions are likely to have included the extraction of food particles, the separation of detritus, or the slowing of water flow for respiration and increased particle encounter. It is hoped that this process will produce a model to test on data from real Peru/Chile plankton profiles, to analyse calorific intake (Ware 1975, 1978) and energy retention (van den Berg *et al.* 1994a) against expected energy requirements (estimated at 5,260 Watts for BMNH P.10000, Peters 1983).

Chapter 10

"...Nonsense upon stilts."

Jeremy Bentham's attack on the French Declaration of Rights
in 'Anarchical Fallacies', 1791.

Chapter 10
Conclusions

- A review of published work and collected material conducted in this study highlighted a lack of individual bones identified, and a history of published taxonomic uncertainty.
- Two specimens (BMNH P.10000 and GLAHM V3363) were identified as particularly important to consider in addition to the type material, due to their unusually extensive nature.
- Archival research tracked down components of BMNH P.10000 misplaced by the host museum, revealing a far more important and complete specimen than previously recognised.
- Material collected outwith Peterborough district was reviewed, with misidentifications noted, and corrected. Hypobranchials and dorsal fin-rays have both been misidentified as tail-spines from a stegosaurian dinosaur. Possible indications of iliophagous behaviour by *Leedsichthys* are assessed. A new locality (Cap de la Hève) is reported that extends the range of *Leedsichthys* into the Upper Kimmeridgian.
- The new Callovian pachycormid taxon *Martillichthys renwickae* is described. The gill basket of *Leedsichthys* is described. Data from both taxa are used to then reanalyse the interrelationships of Pachycormiformes conducted by Lambers (1992). A revised diagnosis of Pachycormiformes is presented.
- The gill rakers of *Leedsichthys* are described. The anomalous 'needle teeth' of PETMG F34 represent either an ontogenetic stage in the development of *Leedsichthys*, or a separate and new taxon.
- Characters based on gill rakers of fish were judged to be unstable and removed from the data matrix for members of the Family Pachycormidae.
- The erection of a second species of *Leedsichthys* (*notocetes*) was judged to be unsafe.
- Analysis on a revised version of Lambers' (1992) character set supported the monophyletic group of edentulous pachycormiformes, but failed to resolve the unstable polyotomy of the 'tusked' pachycormiformes.
- The caudal fin and part of a pectoral fin of *Leedsichthys* are described.
- Sectioning and scaling of postcranial elements from a variety of specimens of *Leedsichthys*, in conjunction with specimen ranking through sizes of individual bones, produced a consistent pattern of length-at-age estimates that are comparable to those of modern-day oceanic suspension-feeding chondrichthyans.
- The initial identifications of bones in the type material of *Leedsichthys* by Arthur Smith Woodward have been revised, with new cranial and postcranial features identified, as a

prelude to the full osteological description that will result from the preparation of specimen PETMG F.174.

- Curvature of unknown elongated bones is used to distinguish and interpret their likely meristic character.
- Length-at-age estimates of *Leedsichthys* are used as a basis for interpretation of its ecology and ecomorphotype.
- The shape and construction of the tail is used to interpret the locomotive abilities of *Leedsichthys*.
- The functions of the gill rakers are assessed with regard to likely optimum feeding speed, and grade of nutrient that could be extracted. This forms the basis for further work on reconstructing the ultra structure of the gill raker from cut sections, acetate peels and CT scans.

Appendices

It was six men of Hindostan, to learning much inclined,
Who went to see the elephant, (though all of them were blind)
That each by observation might satisfy his mind.

The *first* approached the elephant and happening to fall
Against his broad and sturdy side at once began to bawl,
"Bless me, it seems the elephant is very like a wall."

The *second*, feeling at his tusk, cried, "Ho, what have we here?
So very round and smooth and sharp? To me ``tis mighty clear
This wonder of an elephant is very like a spear."

The *third* approached the animal and happening to take
The squirming trunk within his hands, then boldly up and spake,
"I see," quoth he, "the elephant is very like a snake."

The *fourth* stretched out his eager hand and felt about the knee.
"What most this mighty beast is like is mighty plain," quoth he."
'Tis clear enough the elephant is very like a tree."

The *fifth* who chanced to touch the ear said, "Even the blindest man
Can tell what this resembles most; deny the fact who can,
This marvel of an elephant is very like a fan."

The *sixth* no sooner had begun about the beast to grope,
Then seizing on the swinging tail that fell within his scope,
"I see," cried he, "the elephant is very like a rope."

And so these men of Hindostan disputed loud and long,
Each in his own opinion exceeding stiff and strong,
Though each was *partly* in the right and *all were in the wrong*.

Moral:
So oft in theologic wars, The disputants, I ween,
Rail on in utter ignorance Of what each other mean,
And prate about an Elephant Not one of them has seen!

'The Blind Men and the Elephant' John Godfrey Saxe, 1889.

Appendix I

LIST OF CHARACTERS AND CHARACTER STATES

Figure 5.13 is based on the features listed below. [0] represents the plesiomorphic character state and [1], [2], [3] the apomorphic character states. For further discussion see Lambers 1992.

1) Rostrodermethmoid longer than lower jaw symphysis, instead of shorter. [0] short; [1] elongated beyond lower jaw symphysis.
2) Rostrodermethmoid dentition. [0] simple marginal teeth; [1] tusk-like and outward-projecting teeth; [2] absent.
3) Premaxillary dentition. [0] uniform; [1] one or more larger than majority; [2] no premaxilla.
4) Angle of Premaxillary dentition. [0] not placed obliquely; [1] placed obliquely; [2] no premaxillary teeth.
5) Dentary dentition form. [0] uniform; [1] anterior are procumbent; [2] teeth absent.
6) Dentary dentition rows. [0] single row only; [1] marginal plus internal row; [2] no teeth.
7) Gill raker 'needle-teeth'. [0] absent; [1] present.
8) Skull boss at back of roof. [0] no boss; [1] boss present; [2] boss projecting over parietals.
9) Dorsal/anal fin placement. [0] dorsal fin in front of or equal to anal origin; [1] dorsal fin posterior to anal origin; [2] no anal fin.
10) Pelvic fin. [0] present; [1] absent.
11) Pelvic plate shape. [0] simple, slender; [1] large, rounded, long; [2] absent.
12) Anal fin shape. [0] triangular; [1] falcate and extended.
13) Caudal fin segmentation. [0] segmented; [1] unsegmented.
14) Double row of supraneurals. [0] no double row, single row only; [1] double row present.
15) Ossification of centra. [0] no centra; [1] chordacentra only.

Lambers' 16 apomorphies of pachycormids as a discrete group (see Lambers 1993 for further discussion):
16) Anterior part of skull roof formed by median rostrodermethmoid. [0] False; [1] True.
17) Dentigerous anterodorsal border of mouth formed by rostrodermethmoid. Although Lambers (1992) established this character as an apomorphy for pachycormids, this character is not true for *Martillichthys*. [0] False; [1]True.

18) Nasals separated by rostrodermethmoid. Although Lambers (1992) established this character as an apomorphy for pachycormids, this character is not true for *Martillichthys*. [0] False; [1]True.

19) Supramaxilla posterodorsal to maxilla. [0] False; [1] True.

20) Lower jaw without elevated coronoid process. [0] False; [1] True.

21) Dorsal border of lower jaw with elevation opposite premaxilla. [0] False; [1] True.

22) Lower jaw articulating far behind orbit. Although Lambers (1992) established this character as an apomorphy for pachycormids, this character is not true for *Martillichthys*. [0] False; [1]True.

23) >=6 infraorbitals behind orbit. [0] False; [1] True.

24) Infraorbitals at posteroventral corner of orbit not expanded posteriorly/1 infraorbital below orbit. [0] False; [1] True.

25) Dermosphenotic forms dorsal border of orbit. [0] False; [1] True.

26) 2 large plate-like posteriorly expanded suborbitals. [0] False; [1] True.

27) Pectoral fin scythe-like, fin-rays only segmented distally. [0] False; [1] True.

28) Pectoral fins bifurcating asymmetrically in a Y-fashion. [0] False; [1] True.

29) Uroneurals of a peculiar kind. Although Lambers (1992) established this character as an apomorphy for pachycormids, this character is not true for *Martillichthys*. [0] False; [1]True.

30) Hypural plate present. Although Lambers (1992) established this character as an apomorphy for pachycormids, this character is not true for *Martillichthys* or *Leedsichthys*. [0] False; [1]True.

31) Very small rhombic scales. Although Lambers (1992) established this character as an apomorphy for pachycormids, this character is not true for *Martillichthys* or *Leedsichthys*. [0] False; [1]True.

Appendix II

RANGES OF TAXA USED

Outgroup/*Caturus* Range Upper Triassic to Lower Barremian *or* 228.0 to 125.0 Ma

Sauropsis Range Toarcian, Tithonian, Callovian, Kimmeridgian

Euthynotus Range Toarcian

'*Hypsocormus macrodon*' Range Tithonian
-Lambers (1992) notes that the characters of dorsal/anal fin position, segmentation in pectoral fin and character of pelvic plate make it unlikely to be congeneric with *Hypsocormus*.
-Yabumoto (2005) has diagnosed this species as extending into the Neocomian, based on teeth.

Orthocormus Range Tithonian Kimmeridgian

Hypsocormus insignis Range Tithonian, and *leedsi* Callovian

Pseudoasthenocormus Range Tithonian

Protosphyraena Range Middle Cenomanian to Campanian *or* 99.6 to 70.6 Ma

Pachycormus Range Toarcian

Saurostomus Range Toarcian

Asthenocormus Range Tithonian

Leedsichthys Range Callovian-Kimmeridgian

'Taxon 13' Range Callovian (under description)

Appendix III

EXTENDED AND REVISED CHARACTER LIST

List of characters and character states. [0] represents the plesiomorphic character state and [1], [2], [3] the apomorphic character states. For further discussion see Lambers 1992. For the analysis presented in fig. 6.29,6.30. Characters 3 and 4 were combined, and character 7 omitted.

1) Rostrodermethmoid longer than lower jaw symphysis, instead of shorter. [0] short; [1] elongated beyond lower jaw symphysis.
2) Rostrodermethmoid dentition. [0] simple marginal teeth; [1] tusk-like and outward-projecting teeth; [2] absent.
3) Premaxillary dentition. [0] uniform; [1] one or more larger than majority; [2] no premaxilla.
4) Angle of Premaxillary dentition. [0] not placed obliquely; [1] placed obliquely; [2] no premaxillary teeth.
5) Dentary dentition form. [0] uniform; [1] anterior are procumbent; [2] teeth absent.
6) Dentary dentition rows. [0] single row only; [1] marginal plus internal row; [2] no teeth.
7) Gill raker 'needle-teeth'. [0] absent; [1] present.
8) Skull boss at back of roof. [0] no boss; [1] boss present; [2] boss projecting over parietals.
9) Dorsal/anal fin placement. [0] dorsal fin in front of or equal to anal origin; [1] dorsal fin posterior to anal origin; [2] no anal fin.
10) Pelvic fin. [0] present; [1] absent.
11) Pelvic plate shape. [0] simple, slender; [1] large, rounded, long; [2] absent.
12) Anal fin shape. [0] triangular; [1] falcate and extended.
13) Caudal fin segmentation. [0] segmented; [1] unsegmented.
14) Double row of supraneurals. [0] no double row, single row only; [1] double row present.
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Lambers' 16 apomorphies of pachycormids as a discrete group (see Lambers 1993 for further discussion):
16) Anterior part of skull roof formed by median rostrodermethmoid. [0] False; [1] True.

17) Dentigerous anterodorsal border of mouth formed by rostrodermethmoid. Although Lambers (1992) established this character as an apomorphy for pachycormids, this character is not true for Taxon 13. [0] False; [1]True.

18) Nasals separated by rostrodermethmoid. Although Lambers (1992) established this character as an apomorphy for pachycormids, this character is not true for Taxon 13. [0] False; [1]True.

19) Supramaxilla posterodorsal to maxilla. [0] False; [1] True.

20) Lower jaw without elevated coronoid process. [0] False; [1] True.

21) Dorsal border of lower jaw with elevation opposite premaxilla. [0] False; [1] True.

22) Lower jaw articulating far behind orbit. Although Lambers (1992) established this character as an apomorphy for pachycormids, this character is not true for Taxon 13. [0] False; [1]True.

23) >=6 infraorbitals behind orbit. [0] False; [1] True.

24) Infraorbitals at posteroventral corner of orbit not expanded posteriorly/1 infraorbital below orbit. [0] False; [1] True.

25) Dermosphenotic forms dorsal border of orbit. [0] False; [1] True.

26) 2 large plate-like posteriorly expanded suborbitals. [0] False; [1] True.

27) Pectoral fin scythe-like, fin-rays only segmented distally. [0] False; [1] True.

28) Pectoral fins bifurcating asymmetrically in a Y-fashion. [0] False; [1] True.

29) Uroneurals of a peculiar kind. Although Lambers (1992) established this character as an apomorphy for pachycormids, this character is not true for Taxon 13. [0] False; [1]True.

30) Hypural plate present. Although Lambers (1992) established this character as an apomorphy for pachycormids, this character is not true for Taxon 13 or *Leedsichthys*. [0] False; [1]True.

31) Very small rhombic scales. Although Lambers (1992) established this character as an apomorphy for pachycormids, this character is not true for Taxon 13 or *Leedsichthys*. [0] False; [1]True.

New characters added to dataset:

Numbers of fin-rays were assessed from a variety of specimens. Given that specimens are rarely preserved presenting fins in an entirely unfolded or undamaged fashion, it was felt to be most accurate to assess ranges of ray numbers. The quantities below were felt to reflect the diversities presented by the pachycormid taxa.

32) Caudal ray number. [0] circa 15; [1] circa 25; [2] circa 45.

33) Pectoral ray number. [0] 15-20; [1] 21-26; [2] 27-31.

34) Dorsal ray number. [0] circa 15; [1] circa 25; [2] circa 40.

Given the trend for reduced ossification across the Family Pachycormidae, it seemed reasonable to assess this as a character, using a common meristic element, such as a pleural rib, as an index of degree of ossification in the skeleton of the taxon.

35) Rib ossification: [0] ossified ribs; [1] ribs not ossified/preserved.

EXTENDED DATA MATRIX

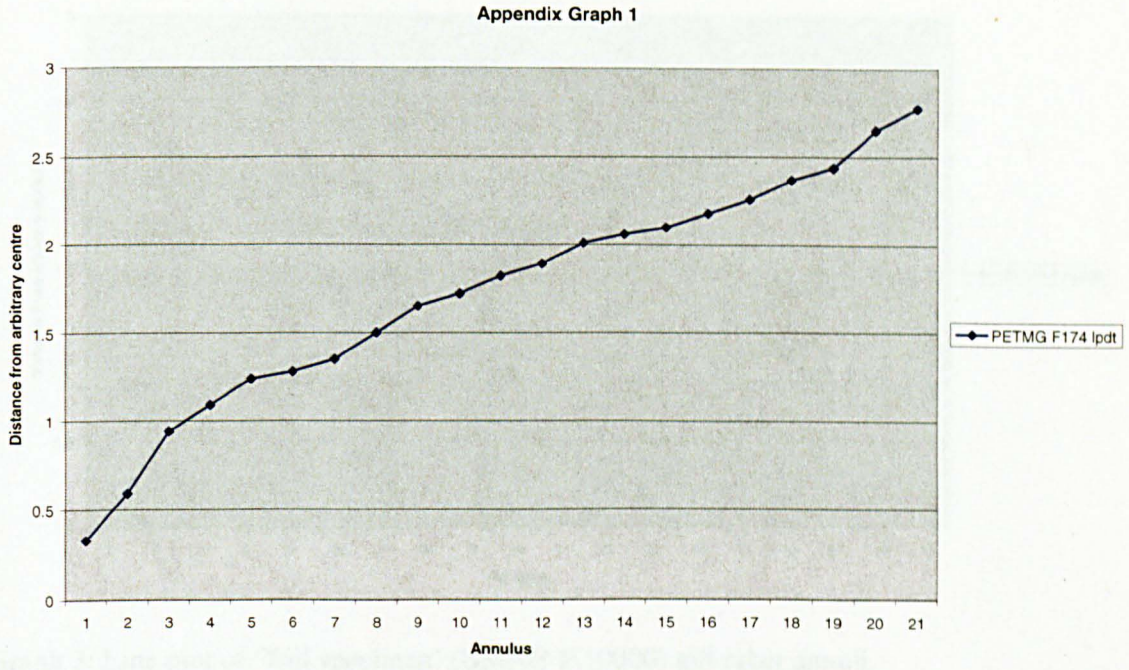
Matrix

Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Caturus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sauropsis	0	0	0	0	0	1	0	0	0	0	0	1	0	0	1	1	1	1
Euthynotus	0	0	0	0	1	0	0	0	1	0	0	1	0	0	1	1	1	1
Hypsocormus macrodon'	0	1	1	1	0	1	0	2	1	0	1	1	0	0	0	1	1	1
Orthocormus	1	1	1	1	1	1	0	2	0	0	1	1	0	0	0	1	1	1
Hypsocormus insignis	0	1	0	0	0	1	0	1	0	0	0	1	0	0	0	1	1	1
Pseudoasthenocormus	0	0	0	0	1	1	0	1	1	0	0	1	0	0	0	1	1	1
Protosphyraena	1	1	1	1	1	1	0	1	?	?	?	?	1	?	0	1	1	1
Pachycormus	0	0	0	0	0	0	0	1	0	1	2	0	0	1	1	1	1	1
Saurostomus	0	0	0	0	0	1	0	1	0	1	2	0	0	1	0	1	1	1
Asthenocormus	0	2	2	2	2	2	1	0	0	?	2	0	1	0	?	1	1	1
Leedsichthys	?	?	?	?	2	2	1	1	?	1	2	0	1	1	0	1	?	?
Taxon 13	0	2	?	?	2	2	0	0	0	0	2	0	1	0	0	1	0	0

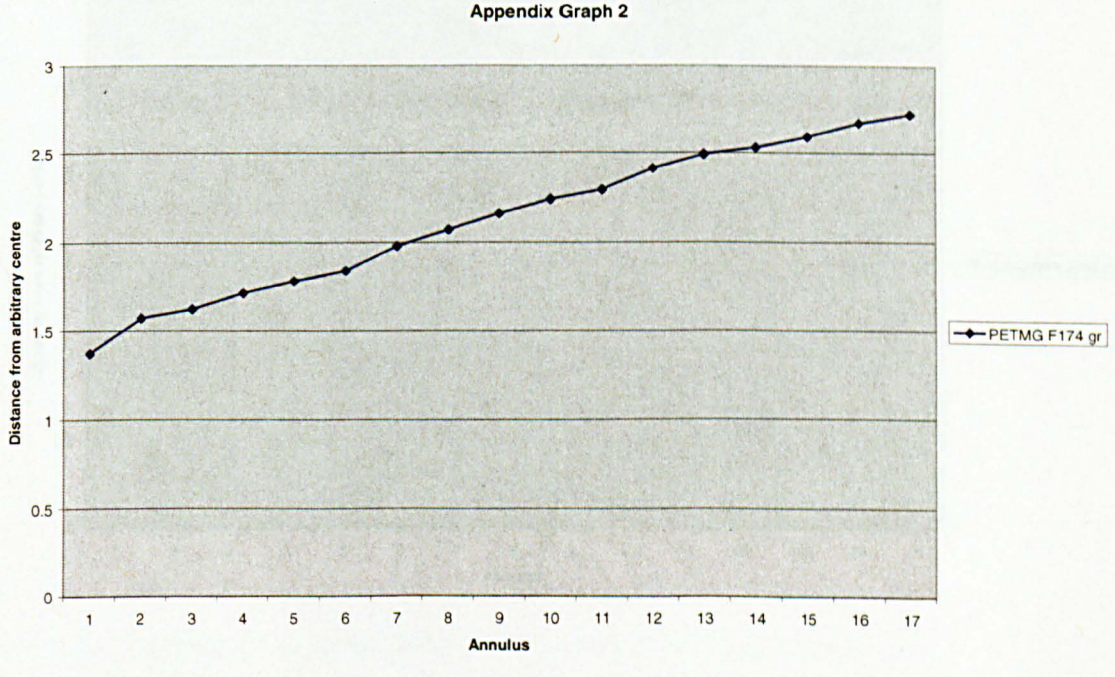
Matrix

Taxa	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
Caturus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sauropsis	1	1	1	1	1	1	1	1	1	1	1	1	1	?	?	?	0
Euthynotus	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1
Hypsocormus macrodon'	1	1	1	1	1	1	1	1	1	1	1	1	1	?	?	?	?
Orthocormus	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	0
Hypsocormus insignis	1	1	1	1	1	1	1	1	1	1	1	1	1	?	?	?	0
Pseudoasthenocormus	1	1	1	1	1	1	1	1	1	1	1	1	1	?	?	?	0
Protosphyraena	1	1	1	1	1	1	1	1	1	1	1	1	1	2	?	?	1
Pachycormus	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	?
Saurostomus	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	2	0
Asthenocormus	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	2	0
Leedsichthys	?	?	?	?	?	?	1	?	1	1	1	0	0	2	0	?	0
Taxon 13	1	1	1	0	1	1	1	1	1	1	0	0	0	2	1	1	0

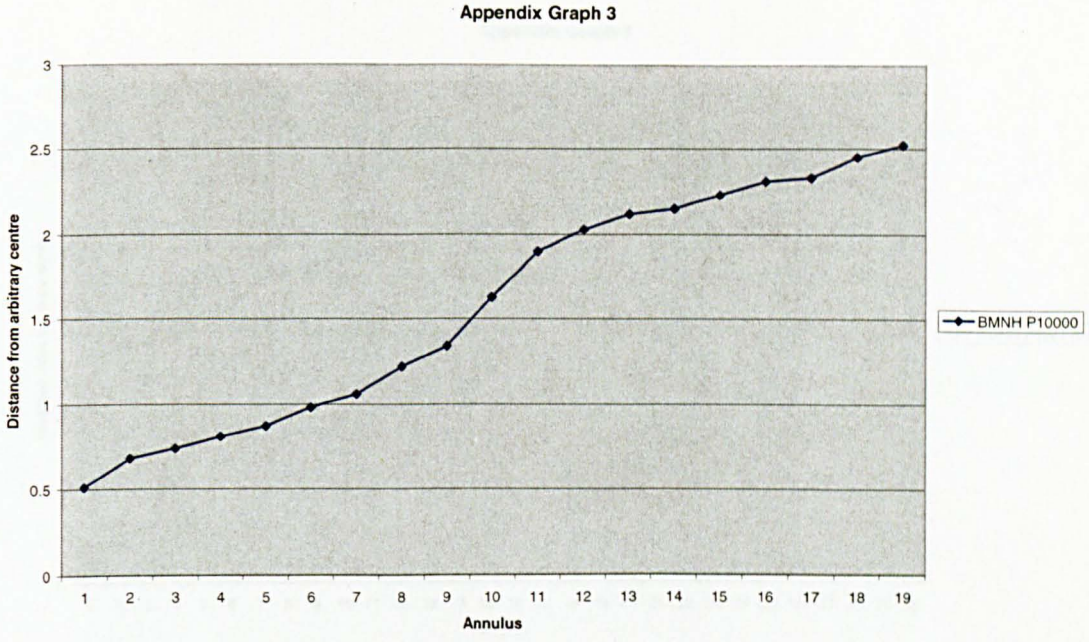
Appendix IV



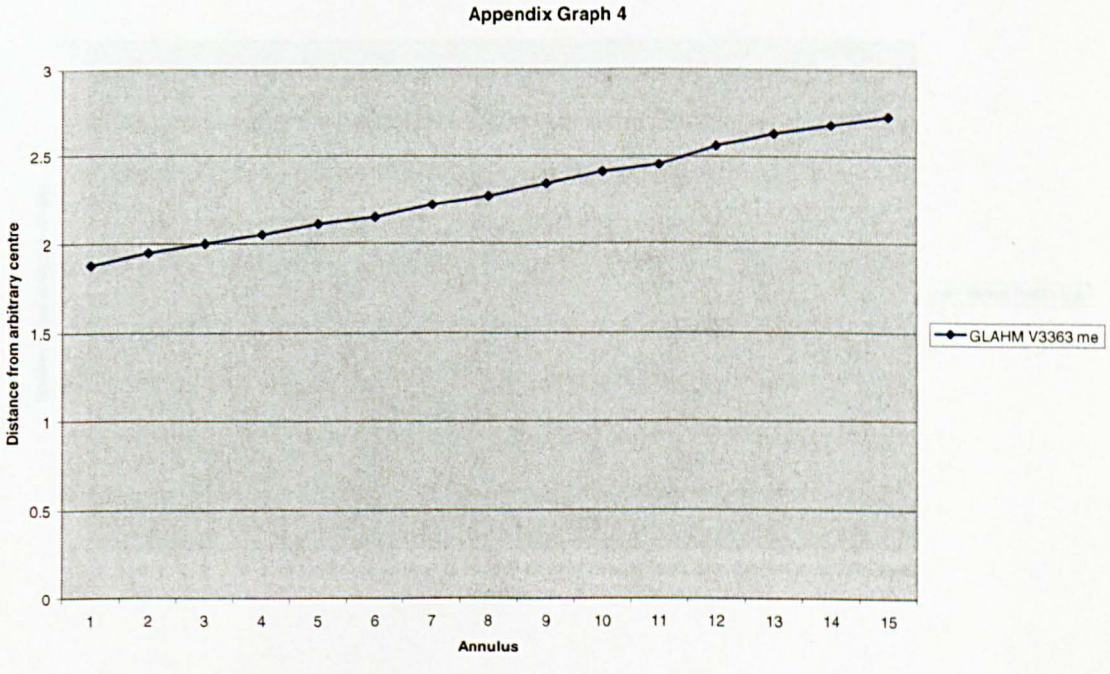
Graph 1: Line plot of 'Ariston' (PETMG F174) lepidotrichium annuli.



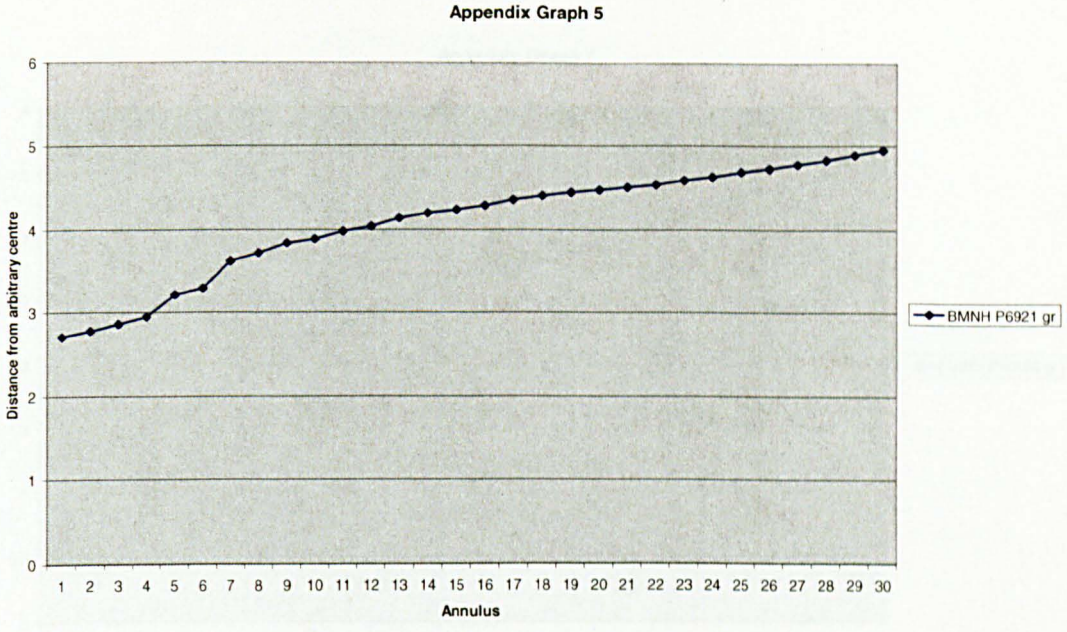
Graph 2: Line plot of 'Ariston' (PETMG F174) gill raker annuli.



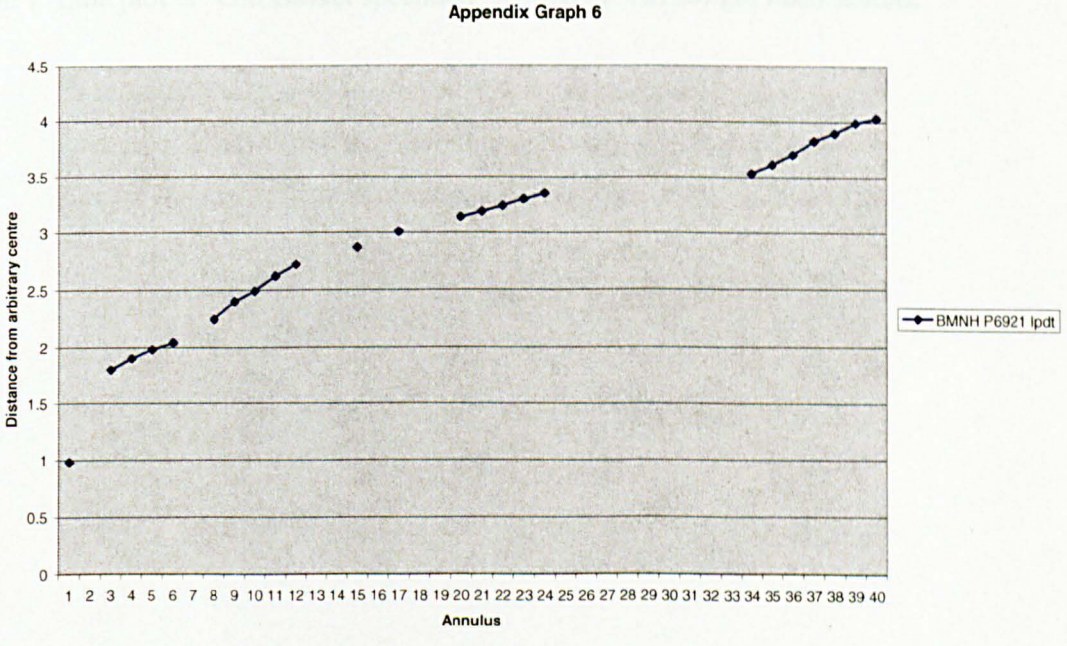
Graph 3: Line plot of 'Tail specimen' (BMNH P.10000) gill raker annuli.



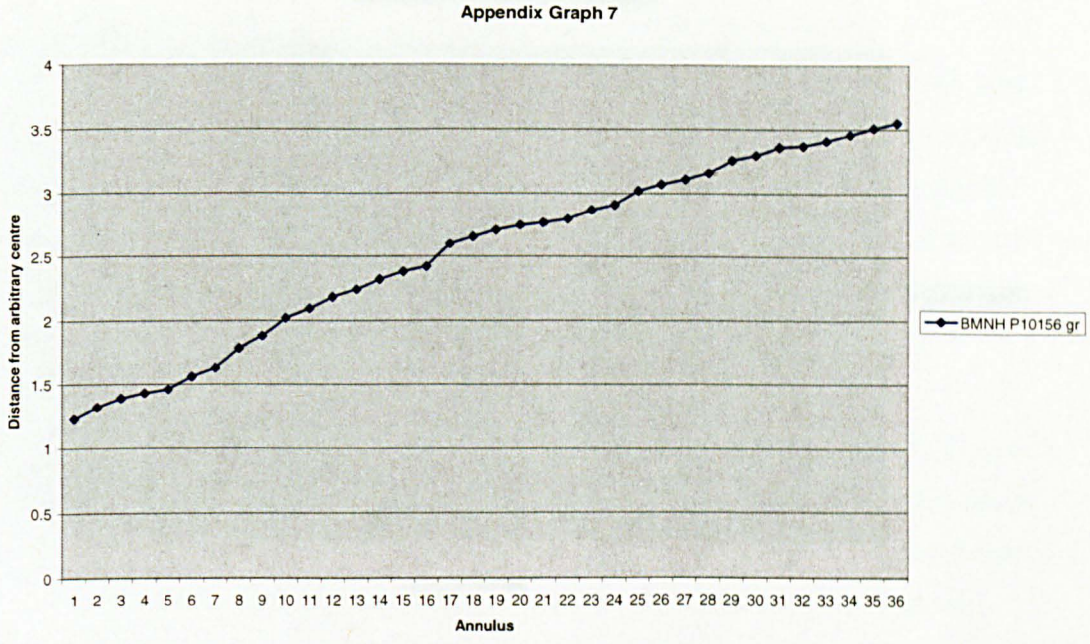
Graph 4: Line plot of 'Big Meg' (GLAHM V3363) meristic element annuli.



Graph 5: Line plot of Holotype (BMNH P.6921) gill raker annuli.

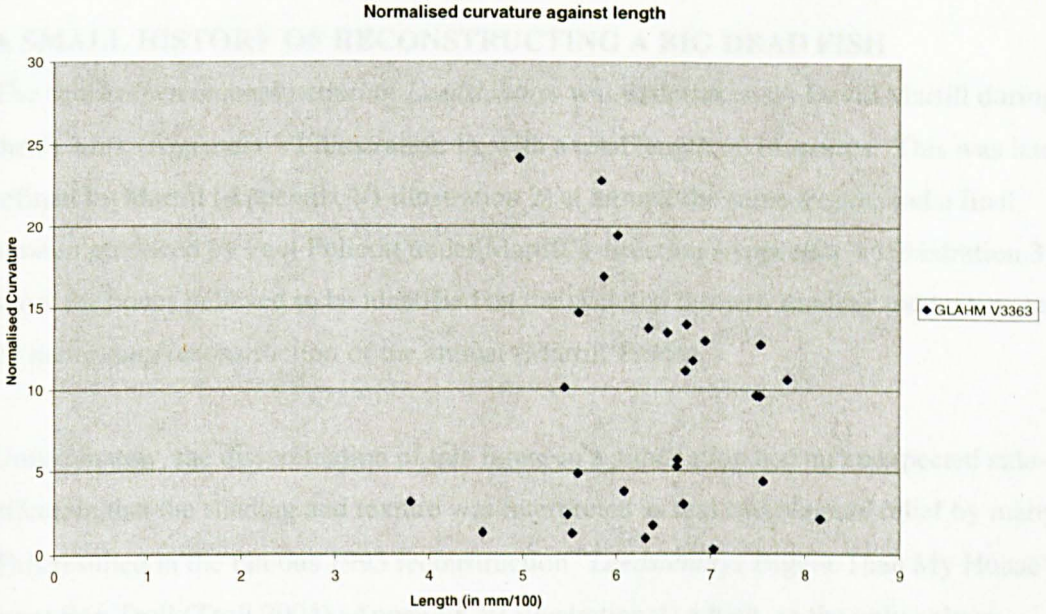


Graph 6: Line plot of Holotype (BMNH P.6921) lepidotrichium annuli.



Graph 7: Line plot of 'Gill Basket specimen' (BMNH P.10156) gill raker annuli.

Appendix V


Normalised curvature against length
Normalised Curvature
Length (in mm/100)
GLAHM V3363
0
5
10
15
20
25
30
0
1
2
3
4
5
6
7
8
9

Appendix VI

A SMALL HISTORY OF RECONSTRUCTING A BIG DEAD FISH

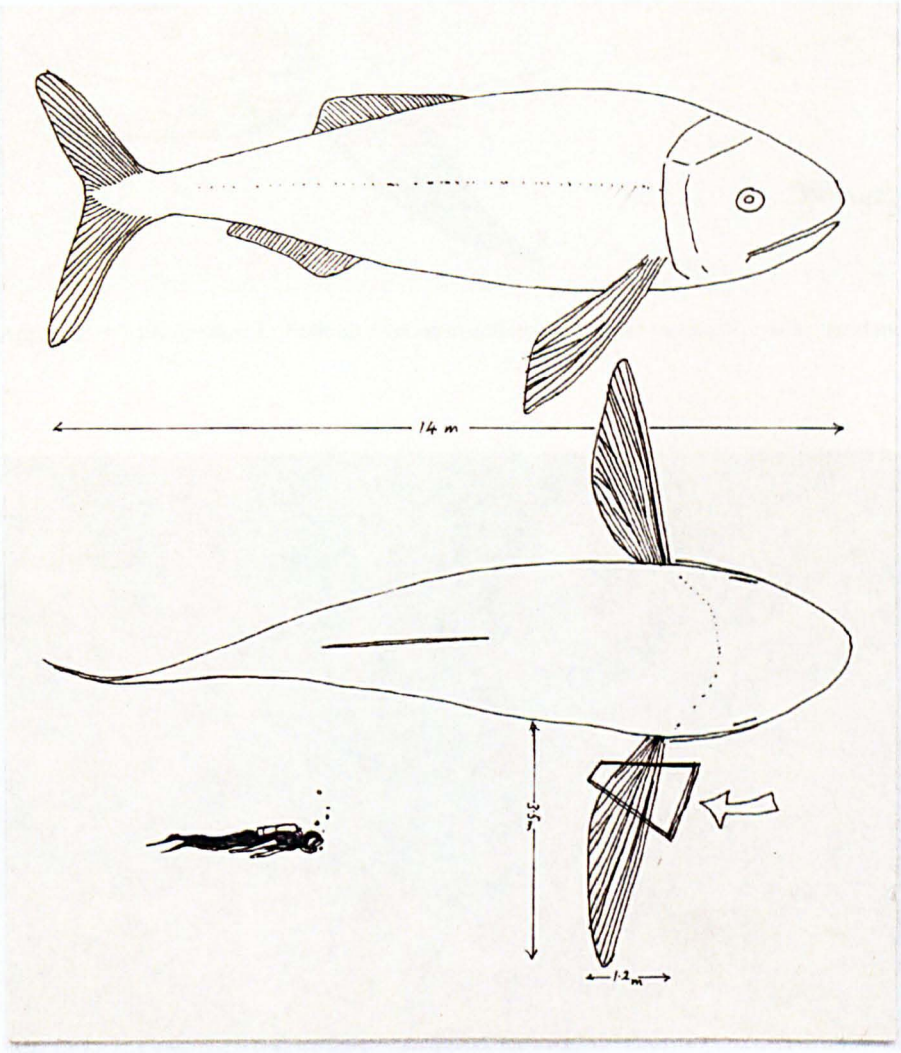
The first known reconstruction of *Leedsichthys* was undertaken by David Martill during his thesis work (Appendix VI illustration 1), with a total length of 14 metres. This was later refined by Martill (Appendix VI illustration 2) at around the same length, and a final version produced by Paul Policott under Martill's direction (Appendix VI illustration 3), to show the bones believed to be identified on the skeleton through shading and texture on a 27 metre long reconstruction of the animal (Martill 1986a).

Unfortunately, the dissemination of this figure in a publication had an unexpected side-effect, in that the shading and texture was interpreted as real osteological relief by many. This resulted in the famous 1995 reconstruction "*Leedsichthys* Bigger Than My House" by artist Ray Troll (Troll 2004) (Appendix VI illustration 4) which, as the only colour reconstruction ever done of the animal, captured the imagination of an Internet audience.

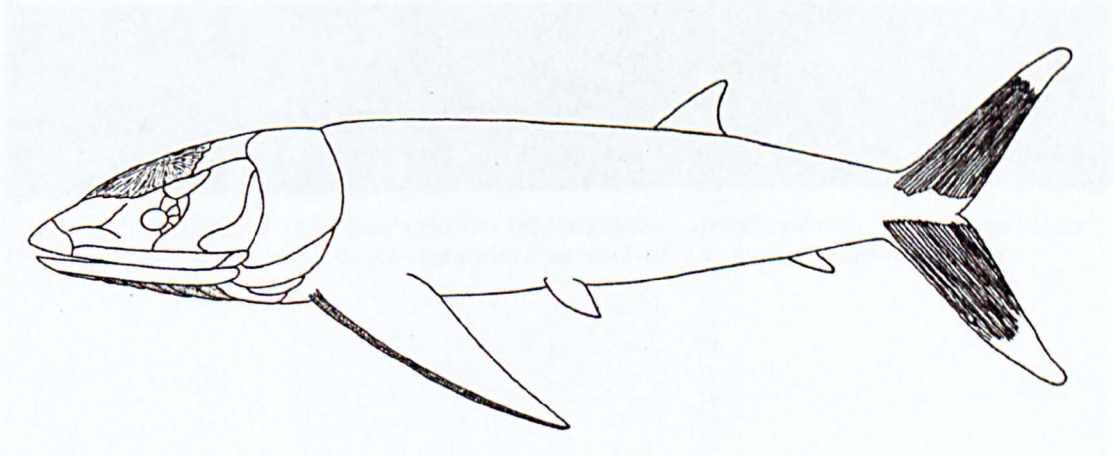
During the course of this project, I have been approached on three separate occasions by the media to advise on a reconstruction of *Leedsichthys*, once for the BBC franchise 'Walking With Dinosaurs', once for the Channel 4 programme 'The Big Monster Dig' that featured the Star Pit excavation (described in Appendix VII/Liston 2006), and once for a piece in the National Geographic Magazine. Both television production companies sadly insisted on making the animal 20-40 metres long, and without bones to support these dimensions, these reconstructions remain woefully inaccurate. Channel 4 did at least attempt to get the overall form correct (even if the length was inflated by a factor of more than four), whereas the BBC appeared to have simply stuck whale flukes on a chameleon.

The National Geographic Magazine enabled me to work with Portuguese artist Pedro Salgado to try and 'build' the animal from scratch, to a realistic size (Appendix VI illustration 5). This was far more satisfactory, but without direct interaction (Salgado was working in Lisbon), slightly frustrating. All three media reconstructions were operating to schedules independent from mine, and wished to design what the reconstruction would look like before the necessary osteological identifications had taken place in order to inform such a design. This was frustrating, and as such, once the necessary osteological identifications had been made, I commissioned the extremely talented palaeoartist Bob Nicholls to work with me in Glasgow in order to reconstruct the animal (Appendix VI illustrations 6a+b). Following some earlier joint work, where we had collaborated on a

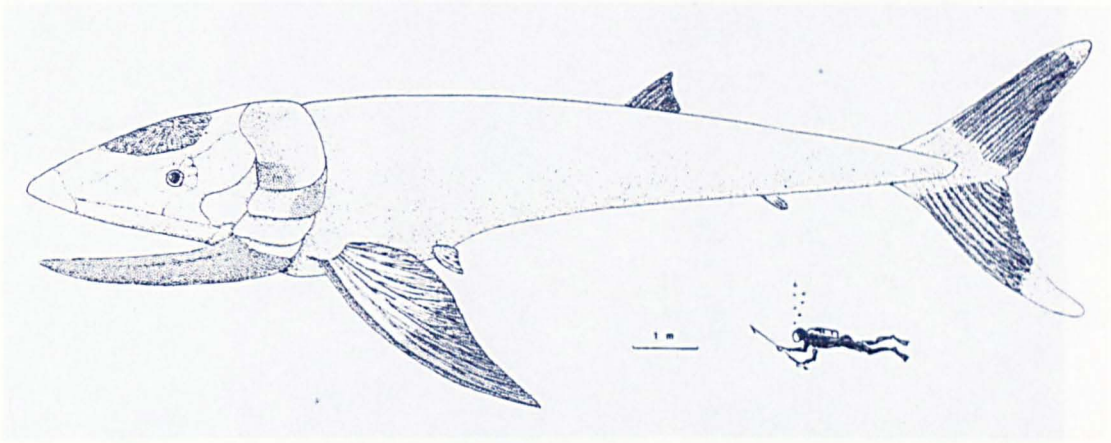
painted reconstruction of 'Big Meg' at just under 20 metres SL (Liston 2006), this model is based on the tail specimen, reconstructing *Leedsichthys* as 12 metres long. Although subsequent work has shown that 8.9 metres is a more likely Standard Length for this individual, this reconstruction remains the most accurate that has ever been produced.



Appendix VI illustration 1: Martill's 14 metre Total Length (=13 metre SL) reconstruction.

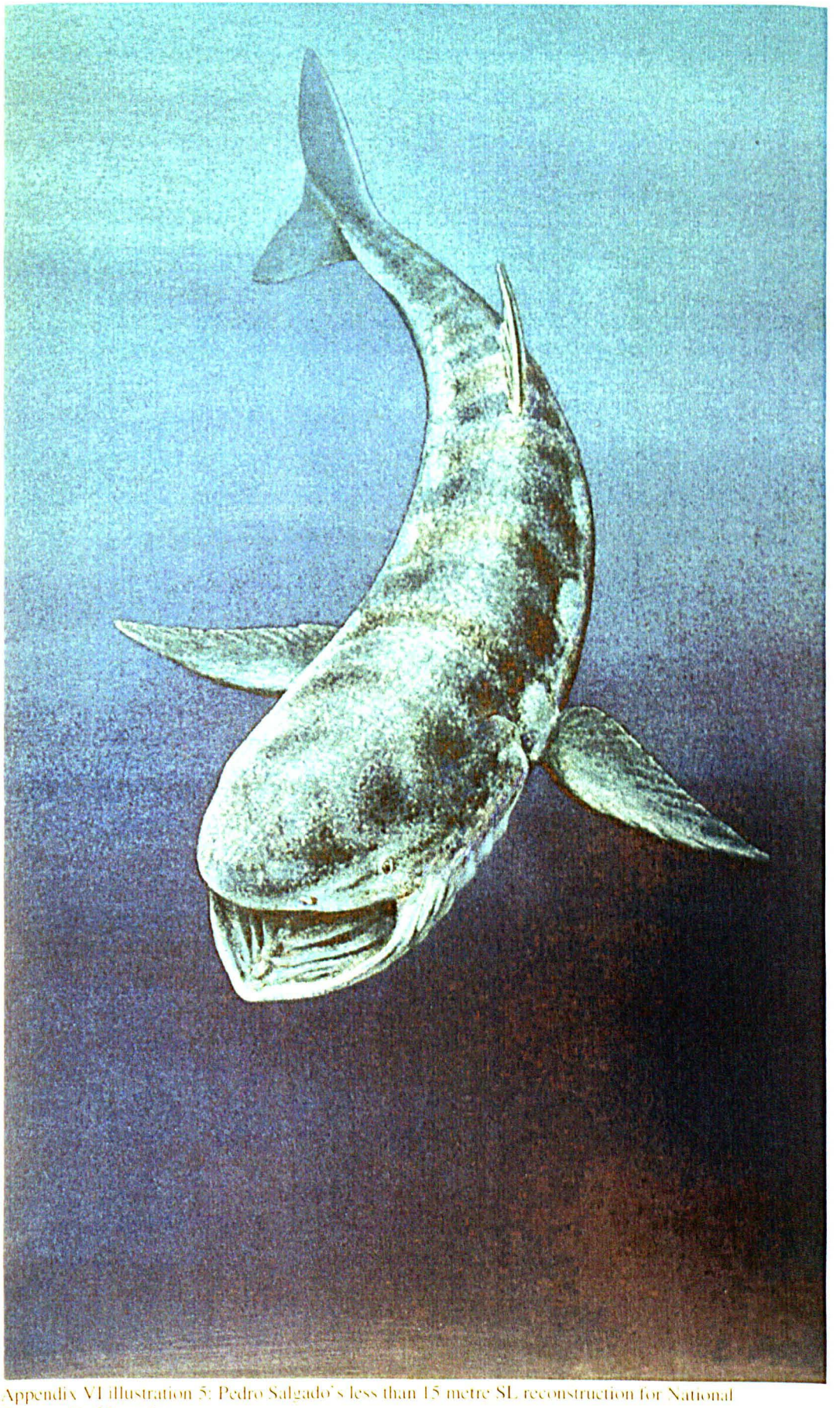


Appendix VI illustration 2: Martill's revised reconstruction, just under 20 metres SL.

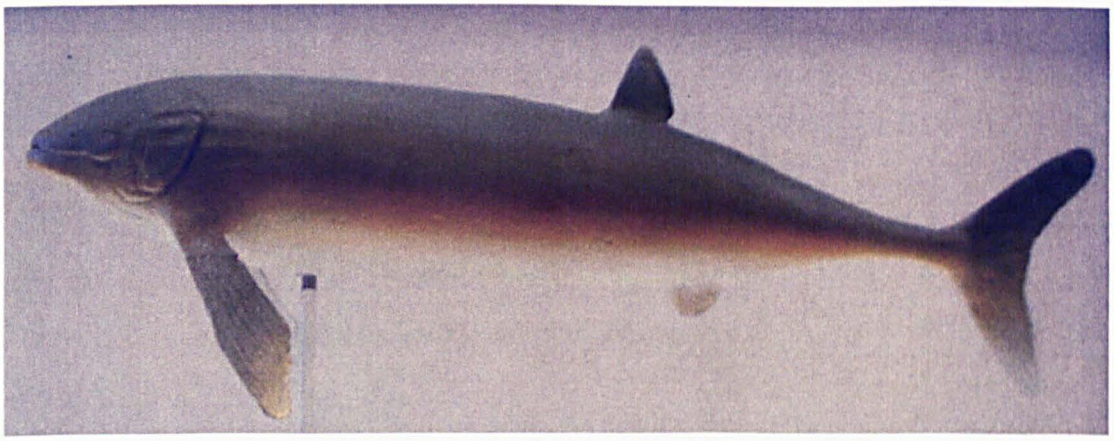


Appendix VI illustration 3.: Policott's reconstruction of over 20 metres SL, under guidance of Martill.

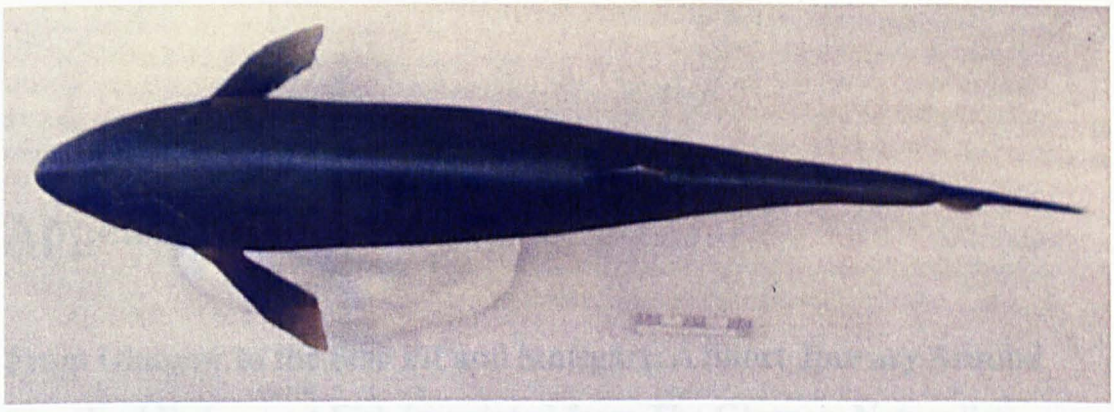
Appendix VI illustration 4. : Ray Troll's glorious and imagination-capturing painting "*Leedsichthys* Bigger Than My House." (1995). Note the textured parietal has 'evolved' into an almost separate lifeform.



Appendix VI illustration 5: Pedro Salgado's less than 15 metre SL reconstruction for National Geographic Magazine.



Appendix VI illustration 6a. : Bob Nicholl's scale model for a 12 metre SL individual, based on BMNH P.10000.



Appendix VI illustration 6b. : Plan view of same model. Scale bar = 50mm.

Appendix VII

From Glasgow to the Star Pit and Stuttgart: A Short Journey Around The World's Longest Fish (reprinted from The Glasgow Naturalist)

Glasgow Naturalist 2006. Volume 24. Part 4. Pages 59-71 .

FROM GLASGOW TO THE STAR PIT AND STUTTGART: A SHORT JOURNEY AROUND THE WORLD'S LONGEST FISH

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ABSTRACT

The Ferrier Fergusson family of Glasgow's West End are more commonly known for their connections to the Tennant family – Henrietta Fergusson and her cousin Margaret Galbraith both married the Tennant brothers who founded the chemical company in their name (Crathorne, 1973). But the sister of Henrietta, Mary Ferrier Fergusson (or 'Ferry' as she was known to her family), married Alfred Nicholson Leeds of Eyebury near Peterborough, who was to become the single collector of the most extensive collection of Jurassic marine reptiles ever. As well as supporting and tolerating the invasion of Alfred's hobby into their living space, Mary also assisted him with the reconstruction of the often fragmentary fossil remains. Her efforts are in particular noted, with regard to the tail of the bony fish *Leedsichthys problematicus* (named in Alfred Leeds' honour), which it took them some nine months to glue together from its thousands of excavated fragments (Leeds, 1956). Following Alfred's death in 1917, Mary requested that the remainder of his collection go to her native city, as part of the Hunterian Museum's collections. Included within the material acquired by the Hunterian from the Leeds family is a singularly complete specimen of the fish *Leedsichthys problematicus*, which currently forms the basis of a research project (in part financially supported by the Glasgow Natural History Society's Blodwen Lloyd Binns Bequest fund) into the osteology of this animal. After the commencement of this project, a new specimen was discovered near Peterborough, which has been included within the scope of this work. Nicknamed 'Ariston', this specimen is the first significant find of this animal in Britain in ninety years.

INTRODUCTION

The nineteenth century was a crucible for change. From historical assessments of ancient cultures, to philosophical viewpoints of the universe, many fields were being critically reassessed in the light of new understanding. Even within the Church, voices were raised questioning the literal truth of the Bible, in the controversial 1860 collection of 'Essays and Reviews' by a series of Anglican clerics and theologians (Blackmore & Page, 1989). New feats of engineering and industrialisation were similarly paralleled by changes in theories of the natural world – advances in microscopy had led to new studies and understanding of biological tissues (Liston & Sanders, 2005). The expanding science of palaeontology was starting to pose awkward questions about the natural world in terms not only of the mutability of species, but also of the extinction of species – something that did not sit comfortably with the majority of people's religious beliefs, and their perception of the Great Chain of Being. The cautious assertion by individuals in the eighteenth century that some animals had become extinct (Rolfe, 1985), had led to the instinctive strivings of Chevalier de Lamarck's *Philosophie Zoologique* (Lamarck, 1809) and Robert Chambers' *Vestiges of the Natural History of Creation* (Chambers, 1845). But these ideas were finally cogently expressed in Darwin's *On the Origin of Species by means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life* (Darwin, 1859). Darwin had been berated for the lack of a fossil example of an intermediate animal between two groups (or 'missing link') to demonstrate his theory of organic evolution 'in action' in the fossil record – but within three years the London specimen of *Archaeopteryx* had been revealed to the world, appearing to provide just what Darwin was lacking (Liston, 2000). Increasingly, the scientific world appeared to be moving towards a worldview that had no need of recourse to a deity working towards a 'grand plan', 'intelligent design' or 'final cause'.

Although it received little coverage at the time, the public debate between Archbishop Wilberforce ('Soapy Sam') and Thomas Henry Huxley on 30th June 1860 at the British Association for the Advancement of Science meeting in Oxford has subsequently come to be seen as symbolic of some of the wrenching changes that the Victorian world was going through at the time. In attacking Darwin's work, Wilberforce is alleged to have sarcastically asked Huxley if he was descended from an ape on his maternal or paternal grandparent's side – after countering Wilberforce's objections, Huxley then accused the Archbishop of prostituting his gifts of eloquence in order to undermine a serious scientific discussion: for a clergyman to be taken so publicly to task was indeed a sign that Science was in the ascendancy (Blackmore & Page, 1989). The debate seems to have signalled a shift in focus away from extinction to questions of descent. And as a symbol of the struggle that society was undergoing, the debate has a deeper resonance than that, for the foundations of its venue (the debate was the public inauguration of a building – the Oxford University Museum - paid for, somewhat ironically, with surplus funds from the University Press's Bible account! (Thomson, 2000)) were sunk deep into the Oxford Clay – one of the most highly vertebrate rich fossil sediments of the British Isles, replete with the remains of extinct animals awaiting discovery.

THE OXFORD CLAY

To the northeast of Oxford, but still within this same rich fossiliferous sediment, was a geographical area in which great surges in knowledge of ancient animal life were to be symbiotically linked with parallel industrial development - the Fenland around Peterborough. It began with an auctioned sale of land around Fletton (just south of Peterborough) – 400 acres were sold on 23/6/1877, and a series of individuals from a diverse group of trades decided to try their hand at producing bricks from the 'brick clay' of this land. Within four years, it had been noted that the deeper clay of the Peterborough area (the Lower Oxford Clay, lying beneath the superficial callow clay more traditionally dug) had an extremely high organic content, which meant that no additional coal or carbon was needed to be imported to fire the bricks – in essence, this 'clay that burns' was self-firing, and in removing the need for the additional expense of shipping in coal for the kilns, Fletton bricks became significantly cheaper, and thus hugely popular. It was this that changed the trend of clay digging from being a small-scale (often family-based) seasonal business, to a large-scale year round industrialised process. This meant that even more land around Peterborough came up for sale, and the landscape was swiftly transformed, with forests of kiln chimneys strewn across the landscape. Although initially excavated by hand with teams of men wielding 2 metre crowbars, this gradually gave way with the rise in demand from 1890 to industrial machinery and mechanical excavators, which more or less dominated the few pits that remained active during the Great War (Hillier, 1981).

By and large, it is essential for human (rather than mechanised) diggers to be employed to dig the clay, in order to observe fossils as they appear and prevent them from being destroyed during clay excavation - as noted by the renowned palaeontologist W. E. Swinton (in the foreword to Leeds, 1956). From this point of view, the optimum historical period for retrieval of fossils, is defined by the peak period of clay excavation following the realisation that the Lower Oxford Clay is an exceptionally useful for brick manufacture (circa 1881), until the time that the industry switches to being fully mechanised, around the end of the war (Leeds, 1956). Throughout this period, one key figure was abroad in Peterborough, collecting the marine fauna from the Jurassic seabeds represented by the Oxford Clay. He had collected such material in earlier years prior to large-scale excavation, and now he was poised to take advantage of the wealth of new material being uncovered every day by the armies of clay diggers now employed in the region. His name was Alfred Leeds.

ALFRED NICHOLSON LEEDS AND MARY FERRIER FERGUSSON

On Tuesday 19th October, 1875, a marriage took place at 11, Grosvenor Terrace (Fig. 1), Glasgow, between the young daughter of city merchant Alexander A. Fergusson, and Alfred Nicholson Leeds Fig. 2), a gentleman farmer living on the fens east of Peterborough. Mary Ferrier Fergusson was embarking on a wedded relationship with a man destined to become one of the world's greatest collectors of fossil Jurassic reptiles. She would also be, in equal part, a preparator and conservator of the bones of these animals from the Middle Jurassic Oxford Clay. In the twenty fifth year of their marriage (as recorded by the second of their five sons, Edward Thurlow Leeds (Leeds, 1956)), they spent nine months in cleaning and gluing together the many thousands of fragments that made up the tail of what was certainly the largest ever bony fish, *Leedsichthys*, named in honour of her husband (Fig. 4). Her palaeontological contribution thus went far beyond the perhaps typical one of the wife of a palaeontologist in the nineteenth century, because beyond simply tolerating the array of drawers of bones strewn around the many rooms of their house in Eyebury (Fig. 3) (east of Peterborough) while they were being worked on by her husband, she was an active supporter and collaborator in his work. Indeed, when Alfred Leeds died on the 22nd August 1917, it became necessary for the family to leave Eyebury soon after, and so she took a hand in the final disposal of the last accumulation of his collection, expressing the wish to Thurlow Leeds that the remainder of the collection of her dead husband (some 450 marine reptile specimens), pass into the care of the University of Glasgow, her native city. This led to the University of Glasgow's Hunterian Museum becoming the owner of the largest collection of Jurassic reptiles from a single collector in Britain, second only in size to the British Museum (Natural History), London.

This was a prodigious achievement: although the British Museum had, during Alfred's lifetime, been the main beneficiary of his collecting, having first refusal on any of the material that he found, most of the material that the British Museum had declined had passed through the hands of the dealer Stürtz of Bonn (between 1897 and 1911), to spread not simply throughout Europe, but around the globe (Leeds, 1956). The Hunterian's acquisition of this final bulk component of his collection meant that, in numerical terms at least, the Hunterian held the largest single collection of Alfred Leeds' material in the world. By the time of this purchase, the Hunterian Museum, along with the rest of the University of Glasgow, had moved from its Old College city centre site into Glasgow's West End, some 5 minutes walk from where Alfred and Mary had married, in Mary's family's home of 11, Grosvenor Terrace, at the head of Byres Road. This meant that for any future trips she made to see her family in Glasgow, the Museum holding the collection from over twenty five years of her late husband's collecting, would be near at hand to visit – and indeed the Hunterian Museum's visitor books record one of her visits on the 21st September 1915.

Prior to this final sale, however, some connections had already existed between Alfred Leeds and the University of Glasgow. A few modest batches of fossil material had already been bought from Leeds by Professor John Walter Gregory (see Fig. 5), the Head of the Geology Department. Gregory appears to have first come into contact with the Leeds Collection when he started work as an Assistant in the Geology Department of the British

Museum (Natural History) in 1887 (Longwell, 1933), during the period in which the initial bulk purchase ('The First Collection') from Alfred Leeds was arriving in that establishment (Leeds, 1956). Gregory later became the first incumbent of the Chair of Geology at Glasgow University in 1904. With that post came the Honorary Curator-ship in Geology for the University's Hunterian Museum, and it was after this that he arranged the purchases for the Hunterian's collections. Included within these were a remarkably complete skeleton of the ichthyosaur *Ophthalmosaurus*, (assembled by Assistant Curator William Robert Smellie, Fig. 6, so that it was on display in the Hunterian Museum from around 1916 until the 1970s, see Fig. 7), and what later turned out to be the most complete specimen of *Leedsichthys* ever collected (Liston, 1999). Now nicknamed 'Big Meg' (Fig. 8), this specimen was first noted by Alfred Leeds in a letter to Arthur Smith Woodward in February 1913 (Leeds, 1913) (Fig. 9, Fig. 10), and was sold to the University of Glasgow in February 1915 (Liston, 2004). Given that Alfred Leeds had traditionally offered first refusal of all his specimens to the British Museum (Natural History) in London, it may seem strange that the BM(NH) did not take the opportunity to purchase this specimen, as it consisted of more than twice the quantity of material as their holotype specimen (BMNH P6921), but archival documentation in the NHM appears to indicate that they had bought a substantial specimen from Alfred Leeds some fifteen years earlier – a specimen that now (despite its size) cannot be entirely confidently located (Liston, 2004; Liston & Noè, 2004). In the light of this, it is perhaps understandable that the BMNH might have let this particular fish 'get away' to Glasgow.

'Meg' is currently the core specimen of a research project based at the University of Glasgow, investigating the virtually undescribed osteology of *Leedsichthys*. To support this research, virtually all known specimens of this taxon have been loaned to Glasgow, a loan that was made financially possible through a generous grant from the Glasgow Natural History Society's Blodwen Lloyd Binns Bequest. The bones of this animal are renowned for being extensive, crushed, broken and fragmentary. In 1889, Arthur Smith Woodward made tentative attempts to understand its skull osteology (Woodward, 1889a, 1889b, 1890), but admitted eight years later that beyond the fin-rays of the tail and the seven and a half centimetre long gill rakers, that no bone had been satisfactorily identified (Leeds & Woodward, 1897). It is believed, because of the unsegmented and bifurcating nature of the fin rays in its tail, that this fish is a member of the Family Pachycormidae. Indeed, in 1916 (Woodward, 1916), Arthur Smith Woodward himself stated with some excitement that he could see a resemblance to *Leedsichthys* bones "in miniature" in the 1.5 metre long specimen of the pachycormid *Saurostomus* from the Holzmaden shale (BMNH P11126, Fig. 11). Arguably the best collection of Jurassic fossil fish specimens lie in the museums in Germany with substantial material from the Holzmaden Posidonienschiefer or lower Jurassic shale of southern Germany, and so a collection visit to these museums (again, generously supported by a grant from the Glasgow Natural History Society's Blodwen Lloyd Binns Bequest) became an essential part of the study.

Why try to see a large number of specimens, as opposed to one well-preserved individual? There are a number of reasons why a comprehensive attempt to see as many specimens as possible of this family of bony fishes would be vital to understanding the skeletal anatomy of *Leedsichthys*, but the central one is this: the skull bones of these pachycormids are so thin and interlock and overlap to such a degree, that individual bones (such as remain of *Leedsichthys*) are extremely hard to discern: it is no surprise that if one looks at the smaller but apparently related genus of *Saurostomus* from the Holzmaden shales that its skull bones are like silk handkerchiefs, so thin that it is hard to tell which bone is lying on top of which (Fig. 12). It is thus only through examining specimens showing skulls in widely differing degrees of disarticulation, that individual bones (and their origins within the overall scheme of the skull) can be determined. Thus, after a few interesting hints from other institutions across Germany (in particular in München and Tübingen), it was of little surprise that the most important clues to the identities of some of the giant skull bones of *Leedsichthys* came from the remarkable Staatliches Museum für Naturkunde in Stuttgart, with its many specimens of both *Pachycormus* and *Saurostomus* from the Holzmaden shale. For the first time, as a result of this examination, it was clear that bones extremely similar to the maxillary (Fig. 13) and dentary (Fig. 14) bones of *Saurostomus* were present in large form in some of the remains of *Leedsichthys* (Fig. 15, 16).

But a more direct aid to the understanding of the skeletal anatomy of *Leedsichthys* had also come to light in the interim.

LEEDSICHTHYS - A NEW SPECIMEN

In July 2001, I received a bone through the post. Not an entirely unusual event in itself, this bone would turn out to be something quite special. It had been found by a Portsmouth Palaeobiology undergraduate (Martill, 2002), working in one of the many brick pits around Peterborough that excavate the Oxford Clay to manufacture bricks (Dawn, 2004). The student, Marcus Wood, had come across the bone protruding from a face that had not been worked by the shale planer since the early nineteen eighties. Another student on the course, Matt Riley, looked at the face independently, and saw a number of smaller bones protruding from the same bed. Fortunately, their course supervisor, Dr. David M. Martill, was also, in collaboration with Dr. Colin Adams of the Institute of Biomedical and Life Sciences, University of Glasgow, co-supervising my postgraduate research on the gigantic Jurassic fish *Leedsichthys*, and so knew to send the bone to me for identification. I was able not only to confirm his suspicion that it was indeed *Leedsichthys*, but also to state that it was likely to be a dorsal fin spine, of the kind mistakenly identified by the German palaeontologist Von Huene as being a tail spine belonging to the stegosaurian dinosaur *Omosaurus* (now *Lexovisaurus*) (Huene, 1901) (see Fig. 17).

The Star Pit at Whittlesey (coincidentally one that Alfred Leeds had himself collected from some 90 years before) was coming to the end of its working life, producing clay for the Hanson Brick Company to turn into bricks. This meant that if a dig were to be organised, it could be run without the health and safety issues surrounding the excavation of material in the same pit as active shale planers, which could prove potentially dangerous. Dr. Martill and myself made plans, and eventually visited the site on the 22nd October 2001, together with Alan Dawn of the Peterborough City Museum, to assess the significance of the find and the potential of the site. We had mixed results from the assessment – on the positive side, we could confirm that, as Matt Reilly had indicated, there were 13 small bones projecting from the cliff, over an 8.5 metre stretch of the same layer (Bed 14 (Hudson & Martill, 1994)) as the one that had yielded the longer dorsal fin spine (Fig. 18). Given the range in sizes of the projecting bones, and that the remains seemed relatively concentrated for a fish estimated to grow anywhere from 10 (Woodward, 1917) to potentially 27.6 metres (as hinted at in the case of one exceptional partial set of remains (Martill, 1986)), it seemed that little transportation or disruption to the skeleton had occurred. This appeared to indicate that a major find, as large as any specimen so far recovered, was hidden within the cliff. On the negative side, an excavation could not be conducted particularly far into a bed with 20 metres of overburden with very much safety. And given the size of the fish, both Dave and I knew that it was likely that a substantial area of the cliff would have to be removed to be confident that we had a chance of recovering everything that we both felt might well be there. It was clear that this would require a heavy piece of excavating machinery, and this would not be cheap to hire. In the worst possible case scenario, we might end up spending a large amount of money to remove a cliff some 20 metres (50 feet) in height, only to find that the fragments that we could see the ends of, were all that was left of the fish – the rest having been removed in the early 1980s and turned into bricks perhaps used for a bathroom extension in Norfolk in the nineteen eighties. But this seemed the least likely result. What was virtually certain was that we had the most significant find of this fish since (according to Natural History Museum archives) February 1913 (Leeds, 1913), and what was extremely likely was that within the cliff was probably the most complete specimen of the fish ever found.

What made attempting to excavate the specimen all the more worthwhile, was that one had never been excavated under the rigour of full scientific procedures, with mapping of the remains before they came out of the ground. The closest to mapped indications of how the bones of *Leedsichthys* had been found, were some doodled sketches contained in a letter from the collector Alfred Leeds to Arthur Smith Woodward of the British Museum (Natural History) in London (Leeds, 1898), and a rough scale-less site map made up retrospectively by a group of German teenagers (as well as Peterborough, the remains of the fish have also been found in Normandie, northern Germany, and Chile) analysing fifteen years worth of photographs that they had taken during their digs (Probst & Windolf, 1993; Michelis *et al.*, 1996). Even if we did prove to be misguided in our expectations of the completeness of this new specimen, the value of the first properly mapped record of the bones of *Leedsichthys* as found, could be immeasurable.

The rarity of such an opportunity was too great to pass on, and by May 2002 Dr. Martill had raised the initial funding for a 2-week dig, led by myself, scheduled for the following month. Dr. Martill would have led the dig himself, but for his intensive work schedule for that summer. Personally, my schedule was also busy - I had a long-planned tour of collections in Germany booked for July - but given the quantity of bone likely to be excavated (based on the quantity of material comprising the most complete specimen currently known, the specimen nicknamed 'Big Meg' in the University of Glasgow's Hunterian Museum), the planned two weeks would be adequate for the excavation necessary. Unfortunately, paperwork problems delayed our starting date, so that the heavy excavator, a 21 tonne Komatsu, could only get access to the site starting on the 24th June (Martill & Liston, 2003). It took fully five days for the extremely skilled driver, Dave Peppercorn, to remove the 20-metre overburden from a roughly 25 metre by 9-metre area of the bed (Fig. 19). He was able to strip the clay beds back to a yellow shell bed layer some 8cm above the bone level (Dawn, 2002), shifting some 10,000 tonnes of material in the process, some of which went to form a platform and slope that our volunteer diggers would later use to work on.

The sky was darkening when the Komatsu excavator finally left the site at the end of that first week, its job done (Fig. 20). I remained to guard the dig over the weekend, to ensure that no opportunistic collectors tried to scavenge material from an abandoned site, while Dr. Martill went to collect his undergraduate volunteer diggers from Portsmouth University for the following Monday morning. I was able, in the fresh 8am daylight of that first Saturday morning, to go down to the newly exposed bed, start to excavate from the edge of the cliff, and take stock of what we actually had. I will never forget that initial period of excavation, seeing the enormous density of bone, far in excess of what we had seen protruding from the edge, and way beyond our expectations. It was clear that we had at least one very completely preserved section of this fish (Fig. 22). Some faulting within the cliff (resulting from slippage of the cliff after being worked by the shale planer in the early eighties) meant that the bone might be limited to that first area (Fig. 21), but still the quantity of bone recovered had already made the expenditure on the excavator worthwhile.

Two days into the following week, I was already running behind schedule for my planned departure for the collection study trip (including the valuable and successful visit to Stuttgart, mentioned earlier). Despite my reluctance to leave the dig at this early stage, it was clear that I had to go. Dr. Martill would take over as acting dig leader in my absence, and despite our joint expectation that everything would soon be finished, he gave me an undertaking that if some well-preserved and associated skull material started appearing, he would ensure that

it was left and not lifted until I had returned and seen it in place. But we were both wrong. When I returned three weeks later, bone was still being exposed, with little sign yet of anything that might be skull material, or an end to the bone material being revealed. The problem was not the usual one on digs, of difficulty in finding bone, but that 'too much' bone was being found – often diggers would complain about how they yearned for areas of clay devoid of bone, so that they knew that at least in one area they had come to an end of the preserved remains. The problems of excavating the material had grown over the days that I had been away. Contrary to appearances when the bed was first cleared, the topography of the clay layer did undulate slightly – and an incautious hand could accidentally go through bone, especially as some elongated rod-like components seemed to be long enough to lie proud of the soft clay layer that the bulk of the bone was held within, so that it projected into the harder slabs of the overlying bed. These topographical problems were compounded by a degree of faulting criss-crossing through the bed that had become apparent when the shell bed had been removed during early hand excavation. Although these faults did not appear to run directly through many bones, and the throw was not too significant (it was never too far from the broken end of one part of a bone to its matching broken surface in an opposing block), this still added complications which might again lead unwary excavators to accidentally excavate through bone. There was a core area of bone that ran in an area about 14 metres by 8, and within that there were many areas that were multi-layered, so that after one layer of bone had been exposed, mapped on to large plastic sheets and removed, another layer came to light. This was particularly problematic and time consuming in an area christened 'Green Bay' (named after the couple that dedicatedly excavated it, Peter and Margaret Green, of the Stamford Geological Society) that was densely filled with gill rakers, and ultimately this could only be resolved by removing roughly 7cm deep slabs of the area, in the hope of full excavation at a later date in laboratory facilities. Also problematic was the bone itself, which baffled seasoned excavators of Oxford Clay reptiles with over twenty years experience, who were entirely unprepared for a fossil animal with so many bones that were often so thin and delicate, yet sometimes exceptionally large and always incredibly fragile. This caused particular problems when trenching around some of the larger bones for plaster jacketing, as there would often be dozens of smaller bones lying around the perimeter, which could unwittingly be destroyed by the incautious digger. The clay needed to be pared away from the bones using dental tools - painstaking and time consuming, but the only way to safely release the bones from this matrix. Traditional methods of applying Paraloid B72 conservation glue had to be distinctly refined – although one could get away with applying thick mixes of this substance to reptile bone in the field, with this fossil fish, the glue simply obliterated the bone and made it extremely difficult to lift from the clay. And yet, in contrast, if the bone did not receive Paraloid B72 very soon after being exposed to the air, it would desiccate and start to break down within a couple of days. This was a particularly significant problem in the first few weeks of the dig when large areas of bone were being exposed faster than they could be protected, and the weather was fluctuating between intense heat and heavy downpours of rain, which alternately baked and flooded the site (see Figs. 23-25).

Although all of these factors were part of an elaborate learning curve for all involved, they also meant that, in conjunction with the quantity of bone being way in excess of what was predictable from existing material, they massively increased the amount of time that the dig took. The new specimen of *Leedsichthys* soon acquired the nickname of 'Ariston', because it simply went 'on and on' (as the old commercial advertisement used to declare). This unpredictability in terms of quantity of material meant that numbers of people available to dig dwindled when the largest amount of bone had to be lifted – after the 26th July, the core team dropped to just three individuals as dedicated diggers on the site. Eventually, the site had to be closed on Thursday 26th September, not because all the bone had been removed, but for two rather more pragmatic reasons. Firstly, the university term was about to commence, which mean that the diggers (both students and staff) needed to return to their various institutions. Secondly, the Hanson Brick Company needed the Portakabin back that they had kindly lent us over the summer in order that we could store the collected specimens in. Both of these factors meant that it was time for the site to be evacuated for that field season. A nine tonne truck was hired for the mammoth job of transporting all of the many hundreds of clay and plaster blocks into more long term storage (Fig. 26).

In August 2003, a small group of diggers reassembled at the Star Pit, to clear the rest of the bones from the exposed bed, for three reasons: firstly to ensure that there was no opportunity for individuals to plunder bones from the bed after the broadcast (planned for a month later) of a television programme reporting the exceptional find (Dawn, 2004); secondly to assess the degree to which bones were continuing into the cliff, and whether it was therefore worth removing more of the cliff in the hope of retrieving more of the same specimen; and thirdly to ensure that should it prove necessary to bring back a heavy digger to take the cliff back further, that there would be no danger that bones left in place on the excavation bed would be damaged by the digger returning. For two weeks, these individuals laboured to clear the remainder of the bone, supported by the Palaeontological Association and the National Museums of Scotland, within a small window of time formed by the availability of individuals to work without jeopardising their own summer project work. The work was made hard by the impact of winter weather, which had homogenised the upper strata, making it difficult to distinguish and separate them during excavation – the 'pen-knife' excavation beloved of the previous year was no longer possible. Following this, the onset of summer had reduced the surface layers to fine flakes of shale, which was difficult to remove cleanly. By the end, the site had been cleared to a degree satisfactory to the diggers, and plans were in place for removal of the cliff. It is planned that, depending on the availability of myself or Dr. Martill, the cliff

removal will not take place until the start of the next field season (2006) – partly so that further bones will be secured safe from potential private collectors within the cliff, and partly because the environmental protection of 20 metres of clay on top of a bed is invaluable: a fresh bed relatively unaffected by weather will be considerably easier to work than one which is exposed to the rigours of the Fens winter.

What have we learned from this remarkable fish specimen (registered with Peterborough City Museum as PETMG F174) – a discovery already described as the most important British vertebrate fossil find since the dinosaur *Baryonyx* was excavated in 1983? The specimen is exceptional in a number of important respects, including quantity of material (over 2,300 bones collected by the end of the 2003 field season, see Fig. 27), the presence of paired bones for the first time in a specimen of *Leedsichthys*, and remarkable clarity of skeletal growth structures on many of its bones, from gill-rakers to hyomandibulae and fin rays. Some of these growth structures superficially resemble growth rings, which hold out some promise of yielding growth data for this animal. With great optimism, Dr. Martill and myself had hoped for some sign of stomach contents as an indicator of diet: the fish has long been regarded as an edentulous suspension feeder like a baleen whale or a basking shark, in part because of its unusually large (over 7.5cm in length) gill-rakers in the absence of any teeth, but some preserved evidence from its gut would help to remove any ambiguity over this. It rapidly became clear that the component of the skeleton that had been preserved within the cliff would not contain this region of its body (that appears to have ended up as part of the aforementioned hypothetical Norfolk bathroom extension), but some small fish vertebrae were preserved within the central mass of gill rakers, which might serve as an indicator of some of the prey items that *Leedsichthys* (perhaps inadvertently) fed upon (see Fig. 28).

In addition to the retrieved remains themselves, and of equivalent importance, is the documentation – a detailed series of plastic mapping sheets (roughly 6 x 2 metres each – see Fig. 29), paper maps, field notes and a host of digital images, all of which make it possible to recreate the disposition of the bones as they were originally found.

Funding is currently being sought for the Herculean task of preparing the bone out of the clay slabs collected – an estimated task of one and a half person years in duration, to fully clean the more than 2,000 bones thus far collected. In the interim, Alan Dawn, the bone plasterer *par excellence* of Peterborough City Museum and Stamford Geological Society, has been working at cleaning occasional bones, but as a part-time volunteer it is slow and arduous work, at a rate of approximately a dozen every three months – a sign of both the scale of the problem, and the difficulty of the work (Fig. 30). Particularly problematic will be the preparation of the most fragile and complex structures, the pectoral fins (Fig. 31), currently embedded in robust plaster jackets and layers of B72 glue (Fig. 32).

It is clear that there is much more of Ariston's bony remains still in the Star Pit, and hopefully funding can also be raised to remove a little more of the cliff (which the skull remains seem to be heading into) and resume the dig armed with an informed and realistic schedule, and a full complement of diggers.

CONCLUDING REMARKS

Alfred Leeds remains a pioneering figure from the nineteenth century 'bone rush' of vertebrate palaeontology. As a single collector, the quality and quantity of his excavated material (in March 1894, just four years after selling his entire collection to the British Museum (Natural History), his newly formed collection was insured with the Insurance Company of North America for £1,000), and its worldwide distribution, is without peer. He personally found no difficulty in reconciling his theological beliefs with Science. Indeed, in a lecture he gave to local people at Glinton School one spring, he criticised 'religious instructors' for failing to keep up to date: "Religion must work with & keep up with science."

We sit at the start of the 21st century, and look back at how much we have learned in the last 150 years. Yet with all our increases in knowledge and understanding, it is humbling to realise how little we have moved forward: as lowly a vertebrate as a fish, whose fossil remains were first described well over a hundred years ago, is little better understood today than it was at the end of the nineteenth century; the recent rise in Christian Fundamentalism has forced creationism back into the school classrooms of the USA and Europe, through the supernatural doctrine of 'intelligent design' (Brumfiel, 2005; Gewin, 2005). A hundred years ago, Alfred Leeds described the cause of the problem as being that the "negligence of churches in not keeping up with [the] times [is the] cause of much unbelief [and] too much going back to the ignorant beliefs, forms, and superstitions of [the] middle ages." Although in many areas, hugely significant progress has been made since the Victorian era, in others, the progress seems a lot harder to discern.

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The dig for Ariston itself had some direct financial benefactors, who have often gone unsung - palaeontological digs rely heavily on the enthusiasm and effort of volunteers, but this excavation was extremely fortunate in being financially supported by a number of bodies, primarily through the gratefully appreciated approaches of Dave Martill - without whom, the dig simply could not have happened. NERC's emergency funding route, and the Aggregate Levy's Sustainability Fund are particular contributors, but the major funder, helping both field seasons (in particular to cover the costs of hiring excavating machinery from R&R Plant Hire, with the highly skilled Dave Peppercorn), was the Palaeontological Association. Other contributors were English Nature, the Stamford Geological Society, the East Midlands Geological Society, and the Friends of Peterborough Museum. The owners of the Star Pit at Whittlesey – Hanson Brick – gave us fantastic hospitality and access to essential facilities as well as the permission to excavate Ariston, and Andy Mortlock was a stalwart point-of-contact. Further help in kind was in particular provided by the Hunterian Museum (University of Glasgow), the National Museums of Scotland and also by the University of Portsmouth - but the most significant contributor in this respect was all the diggers, who gave their time for no remuneration whatsoever - making a total of over 3,000 working hours in the pit over both field seasons. Special mention and thanks go to Tom Challands and Kay Hawkins in this regard. Sarah Earland, Peter and Margaret Green gave particular specialist expertise to the dig. Nick Watts and Adeline Ramage tried hard to make the filming as painless as possible, which was appreciated. Dave Martill has kindly allowed the reproduction of some of the images used in this article.
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Finally, appreciation is expressed to John Wagner and Carlos Ezquerra for coming up with the 'Big Meg'.

INSTITUTIONAL ABBREVIATIONS

GLAHM = Hunterian Museum, The University of Glasgow, Scotland.
SMN ST = Staatliches Museum für Naturkunde in Stuttgart, Germany.
BMNH = Natural History Museum (London), England.
PETMG = Peterborough Museum and Art Gallery, Cambridgeshire, England.
CAMSM = Sedgwick Museum of Geology, Department of Earth Sciences, University of Cambridge, England.

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PLATES AND FIGURES

PLATE 1.

FIGURE 1. Number 11, Grosvenor Terrace, in Glasgow's West End, around the time when Mary's family lived there, at the end of the nineteenth century. The house was only a few minutes walk away from the University of Glasgow's Hunterian Museum. Photograph used by courtesy of the Mitchell Library, Cultural & Leisure Services, Glasgow City Council.
FIGURE 2. Alfred Nicholson Leeds and Mary Ferrier Fergusson, together in a Peterborough photographic studio, around 1875. Image courtesy of Julian Leeds. Copyright resides with the Leeds Family.
FIGURE 3. The Leeds family home at Eyebury. Image courtesy of Julian Leeds, from the unpublished manuscript 'Eyebury and the Leeds collection', 1938/9.
FIGURE 4. The tail (BMNH P.10,000) of *Leedsichthys problematicus*, as displayed in 1937 (NHM-ESL negative number 1660). The span of the tail is 2.74 metres. Thurlow Leeds recalled why it took some nine months to reassemble the "thousands of pieces" of the tail collected: "a packet of fragments representing a length of 3 or 4 inches, and belonging possibly to two original rays, contained on the average (in the slenderer parts) 120 fragments" (Leeds, 1956). By permission of the Trustees of The Natural History Museum (London).
FIGURE 5. Professor John Walter Gregory, Chair of Geology (1904-1929) in the University of Glasgow, and Honorary Curator in Geology for the Hunterian Museum. Photograph © Hunterian Museum, University of Glasgow.
FIGURE 6. Dr. William Robert Smellie, Assistant Curator in Geology, circa 1915. He worked extensively on reconstructing the marine reptiles of Alfred Leeds bought for the Hunterian Museum. Reproduced with kind permission of Valerie Boa, with whom copyright resides.
FIGURE 7. The mounted skeleton of *Ophthalmosaurus icenicus* (GLAHM V1070), as displayed in the Hunterian Museum from about 1916-1966. Picture probably taken between 1916 and 1920 by S. Finland. Photograph © Hunterian Museum, University of Glasgow.
FIGURE 8. The full extent of 'Big Meg' (specimen GLAHM V3363), laid out in a corridor of the Hunterian's main research store. John Faithfull (1.8m) is included for scale.
FIGURE 9. The bone sketched by Alfred Nicholson Leeds in his letter to Arthur Smith Woodward. It is a component of specimen GLAHM V3363 ('Big Meg'). Bone is a 77cm long preopercle.
FIGURE 10. Extract from a February 1913 letter from Alfred Nicholson Leeds to Arthur Smith Woodward, enquiring about a bone of *Leedsichthys* that he had found. (NHM-GL DF100/55/468). By permission of the Trustees of The Natural History Museum (London). Copyright resides with the Leeds Family.

PLATE 2

FIGURE 11. *Saurostomus esocinus* (BMNH P11126), 1.3 metres long.
FIGURE 12. Detail from the skull of BMNH P11126 (field of view is 11cm wide).
FIGURE 13. Skull of SMN ST 52472, clearly showing outline of maxillary.
FIGURE 14. Skull of SMN ST 50736, clearly showing outline of dentary.
FIGURE 15. Maxillary of 'Big Meg' (GLAHM V3363).
FIGURE 16. Dentary of 'Big Meg' (GLAHM V3363).
FIGURE 17. The first bone of 'Ariston' (PETMG F174) – sent for identification after excavation from the Star Pit in 2001. Below is a piece of *Leedsichthys* identified by Friedrich Von Huene in 1901 as a stegosaurian tail-spine (CAMSM J.46873).
FIGURE 18. The *Leedsichthys* locality in the Star Pit. Alan Dawn and David Martill stand next to the quarry face, indicating the 8.5 metre distance over which bone was found on 22nd October 2001. David Martill (right) is pointing at the horizontal bed that the bone was emerging from. A yellow 'X' between them marks where the first bone sample was retrieved from the bed by Marcus Wood.
FIGURE 19. The Komatsu excavator, driven by Dave Peppercorn, obliterating the 20 metre high cliff sitting on top of the fish. © D. M. Martill.

PLATE 3.

FIGURE 20. The author views the newly exposed bed, prior to manual excavation commencing, on 29th June 2002. © D. M. Martill.

FIGURE 21. First excavated area, showing slippage 'fault' to left. Margaret Green for scale. © D. M. Martill.

FIGURE 22. Reconstruction of *Leedsichthys* as an 18 metre fish by Bob Nicholls (September 2003), with line to show the portion of the body (to the left) thought to be contained within the cliff. © Bob Nicholls, Palaeocreations (www.paleocreations.com).

FIGURE 23–25. The site regularly flooded (23) and required to be pumped out (24) before excavation could continue (25).

FIGURE 26. Fish-van: the nine tonne truck filled with plaster jackets containing the bones of the fish. In the foreground is a Channel 4 filmcrew.

PLATE 4.

FIGURE 27. Peter Green's map of the site: each cross marks the corner of a 1 metre square grid, designed and constructed by him, that was utterly invaluable for accurately recording the site. For simplicity at this scale, only the largest components have been included. © Peter Green, 2002.

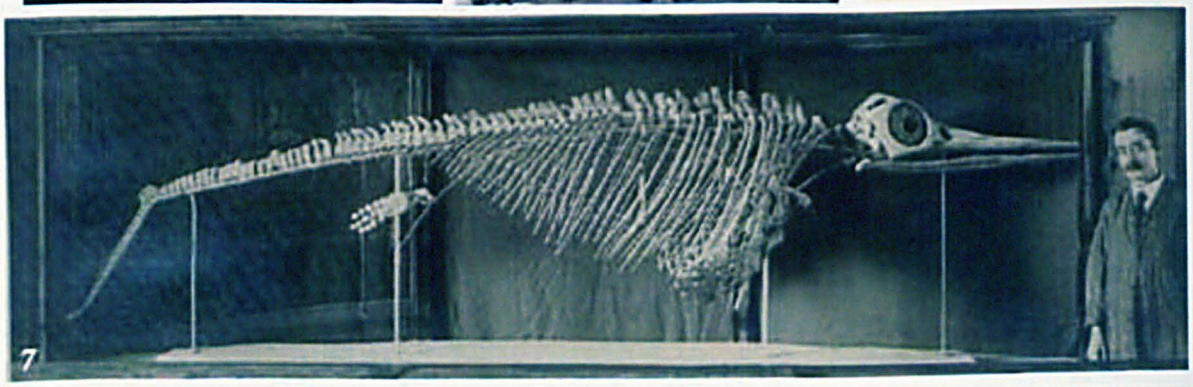
FIGURE 28. Sketch by Bob Nicholls (August 2004) to indicate the indiscriminate ingestion of an extremely large suspension-feeding Jurassic fish. © Bob Nicholls, Palaeocreations (www.paleocreations.com).

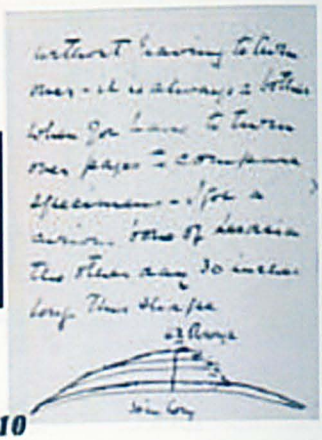
FIGURE 29. Unrolling one of the 18 plastic mapping sheets created to map the finds during the two field seasons. Peter Green (orange hard hat) directs operations. © D. M. Martill.

FIGURE 30. A handful of the more than 2,300 bones retrieved from the Star Pit site. These have been prepared out of their clay matrix by Alan Dawn, of the Peterborough City Museum.

FIGURE 31. The right pectoral fin of Ariston (PETMG F174/10,002), pedestalled prior to being jacketed in plaster for removal. © D. M. Martill.

FIGURE 32. The left pectoral fin (with overlying dermal bones, PETMG F174/10,025) hoisted into the air on the last day of the first field season. © D. M. Martill.





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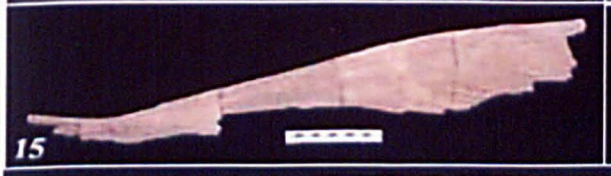

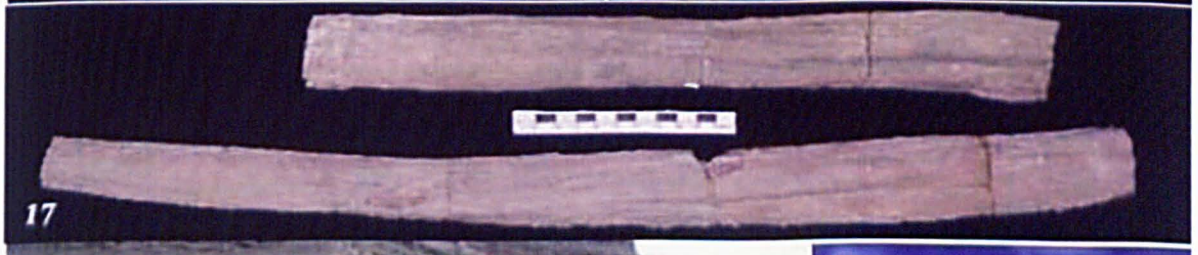

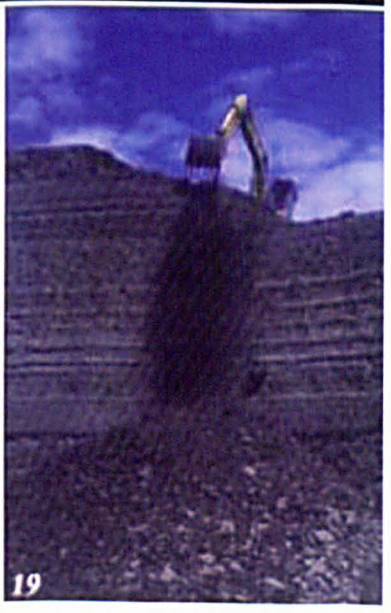

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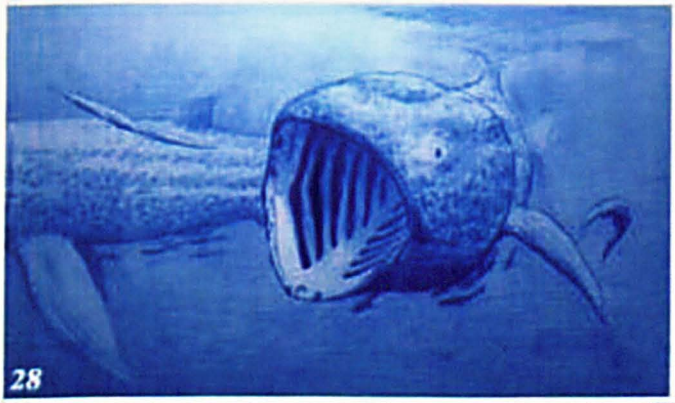

Liston Plate 4.

Appendix VIII

NOÈ, L.F. LISTON, J.J. AND EVANS, M. 2003. The first relatively complete exoccipital-opisthotic from the braincase of the Callovian pliosaur, *Liopleurodon*. (reprinted from *Geological Magazine*)

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The first relatively complete exoccipital-opisthotic from the braincase of the Callovian pliosaur, *Liopleurodon*

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Abstract – A newly recognized left exoccipital-opisthotic of a Callovian pliosaur, derived from the Peterborough or lower Stewarby Members of the Oxford Clay Formation of Peterborough, is described and figured. This isolated bone is tentatively identified as belonging to an 'adult' individual of *Liopleurodon ferox* that is inferred to have had a skull length of 1.26 metres and an overall body length of 6.39 metres.

Keywords: Jurassic, Callovian, Sauropterygia, Plesiosauria, braincases.

1. Introduction

Pliosaur occipital and braincase elements are rarely preserved, and when present are often damaged or obscured by crushing of the cranial roof and suspensorium against the palate (e.g. Andrews, 1895, 1897, 1909, 1913; L. F. Noè, unpub. Ph.D. thesis, Univ. Derby, 2001). The three-dimensional structure of the pliosaur braincase and its associated nerve and blood vessels is therefore problematic to reconstruct. A rare pliosaur exoccipital-opisthotic complex, CAMSM J.27424 (see below for institutional abbreviations), originally mis-identified in the Museum as belonging to the giant filter-feeding fish *Leedsichthys problematicus* Woodward, 1889, is described and interpreted. Although CAMSM J.27424 is an isolated element, its recognition as a large, well-preserved and almost uncrushed exoccipital-opisthotic complex adds significantly to our understanding of pliosaur braincase anatomy. Prefixes for figured and cited specimen numbers denote the following repositories: CAMSM – The Sedgwick Museum, Cambridge; PETMG – Peterborough Museum and Art Gallery, Peterborough; NHM – The Natural History Museum, London; GPIT – Institut und Museum für Geologie und Paläontologie, Tübingen.

2. Locality and horizon

CAMSM J.27424 was collected in 1909 from a brick pit in Whittlesey, south of Peterborough, England. The brick pits in the Whittlesey area (Fig. 1) currently expose the whole of the Peterborough Member and the lowest few metres of the overlying Stewartby Member of the Oxford Clay Formation (Hudson & Martill, 1994). These 'deposit-feeder' shales preserve the *Sigaloceras calloviense* to *Peltoceras athleta* ammonite zones (Martill & Hudson, 1991), and are therefore of Callovian age (161.3 to 157.1 million years ago: Harland *et al.*, 1990). However, whether CAMSM J.27424 originated from the Peterborough Member, or the bottom of the Stewartby Member of the Oxford Clay Formation, cannot be stated definitively. The Stewartby Member is generally considered to be less fossiliferous than the underlying Peterborough Member (Cox, Hudson & Martill, 1992), with Bed 10 of the Peterborough Member (Callomon, 1968) presently identified as the most prolific source of fossil vertebrates in the Peterborough area (Martill, 1986; Hudson & Martill, 1994). However, this is an artefact of modern clay extraction techniques: shale planers are used to remove the clay to a level immediately above Bed 10 of the Peterborough Member, thereby destroying fossils higher in the succession. Older sources indicate that fossils of marine vertebrates have been collected from all levels of the Callovian Oxford Clay Formation in the Peterborough area (e.g. Leeds & Woodward, 1899; Leeds, 1956).

3. The pliosaur braincase

The braincase in Callovian pliosaurs is partially exposed in lateral view through the large temporal fenestrae (Fig. 2), and consists of seven bones: four median and three paired. Dorsally, the supraoccipital (s) surmounts the paired prootics (pr) anteriorly and the paired exoccipital-opisthotics (eo) posteriorly. Each prootic contacts the exoccipital-opisthotic posteriorly, the basisphenoid (bs) anteroventrally, and the basioccipital (bo) posteroventrally. Each exoccipital-opisthotic overlies the basioccipital ventrally, the

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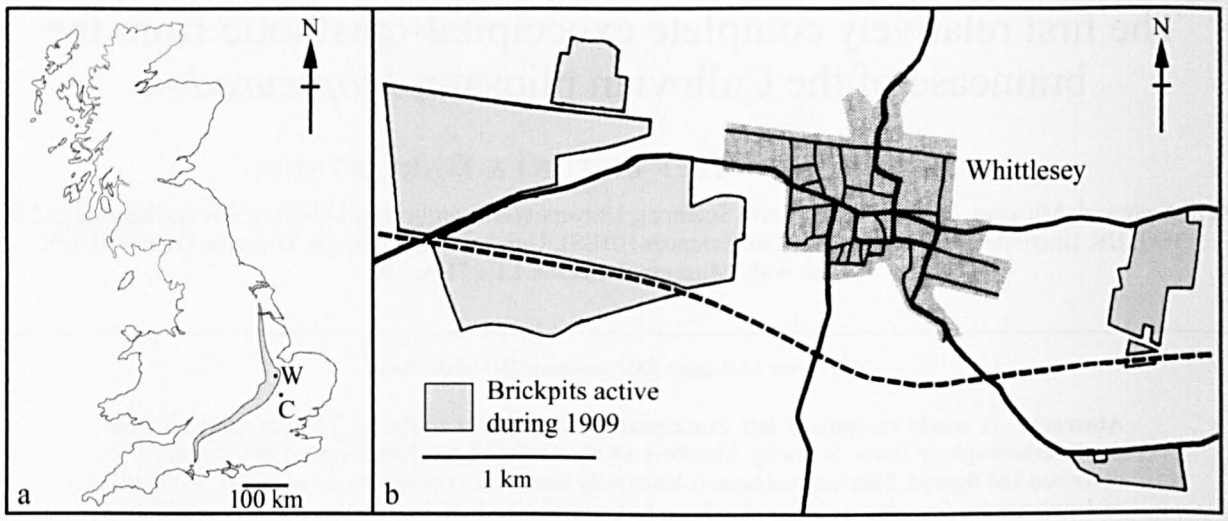

Figure 1. Locality maps. (a) Mainland Britain showing the outcrop of the Oxford Clay Formation in England (after Martill & Hudson, 1991), Abbreviations: C – Cambridge, W – Whittlesey, Cambridgeshire, the location from which CAMSM J.27424 was recovered. (b) Modern extent of the brick pits active in the Whittlesey area and working the Peterborough Member, Oxford Clay Formation during 1909 (modified from Hillier, 1981).

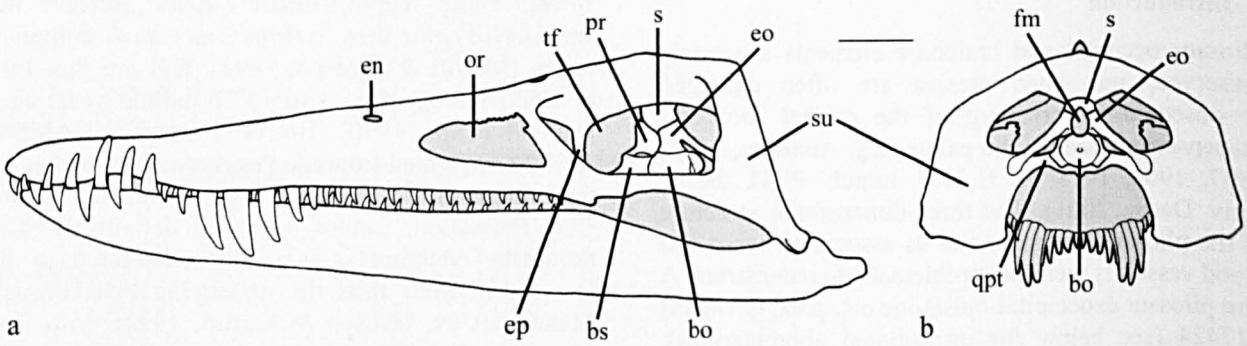

Figure 2. Outline cranial reconstructions of the Callovian pliosaur *Liopleurodon ferox* Sauvage, 1873 to indicate gross morphology and location of dorsal braincase elements in (a) left lateral, and (b) posterior views. Scale bar 100 mm. Abbreviations: bo – basioccipital, bs – basisphenoid, en – external nares, eo – exoccipital-opisthotic, ep – epipterygoid, fm – foramen magnum, or – orbit, pr – prootic, qpt – quadrate ramus of pterygoid, s – supraoccipital, su – suspensorium, tf – temporal fenestra.

basisphenoid contacts the basioccipital posteriorly, and these two bones are under-plated by the sheet-like parasphenoid. Anterolaterally, the epipterygoids (ep) form a pair of pillars extending from the dorsal surface of the pterygoid ventrally, and contact the parietal dorsally. Ventrally, the braincase is underlain by the posterior rami of the pterygoids.

In pliosaurs, as in some other marine reptiles, the exoccipital and opisthotic are fused to form a single bony unit (Williston, 1925; Romer, 1956). Fusion occurs in all members of the Plesiosauria (Brown, 1981), although the line of suture between the two elements may remain visible even in the adult (Andrews, 1897, 1913; Brown, 1981, fig. 36d). The exoccipital-opisthotic consists of a stout, pillar-like body, and a very elongate paroccipital process (the opisthotic was formerly known as the 'paroccipital bone': Williston, 1925). The body of the exoccipital-opisthotic forms the lateral margin of the foramen magnum (fm, Fig. 2b), and is pierced by foramina for the passage of cranial nerves, blood vessels, the perilymphatic duct, and the semicircular canal system of the inner ear (Romer, 1956). The slender paroccipital process provides vital mechanical bracing between the suspensorium and the rear of the braincase.

4. Description

CAMSM J.27424 is the left exoccipital-opisthotic of a pliosaur. The exoccipital and opisthotic elements are

Figure 3. Photographs of CAMSM J.27424 in (a) dorsal, (b) medial, (c) ventral, (d) lateral, (e) anterior, and (f) posterior views; for interpretive drawings see Figure 4. Arrows give anatomical orientations, scale bar = 100 mm. Abbreviations: ant – anterior, dor – dorsal, med – medial.

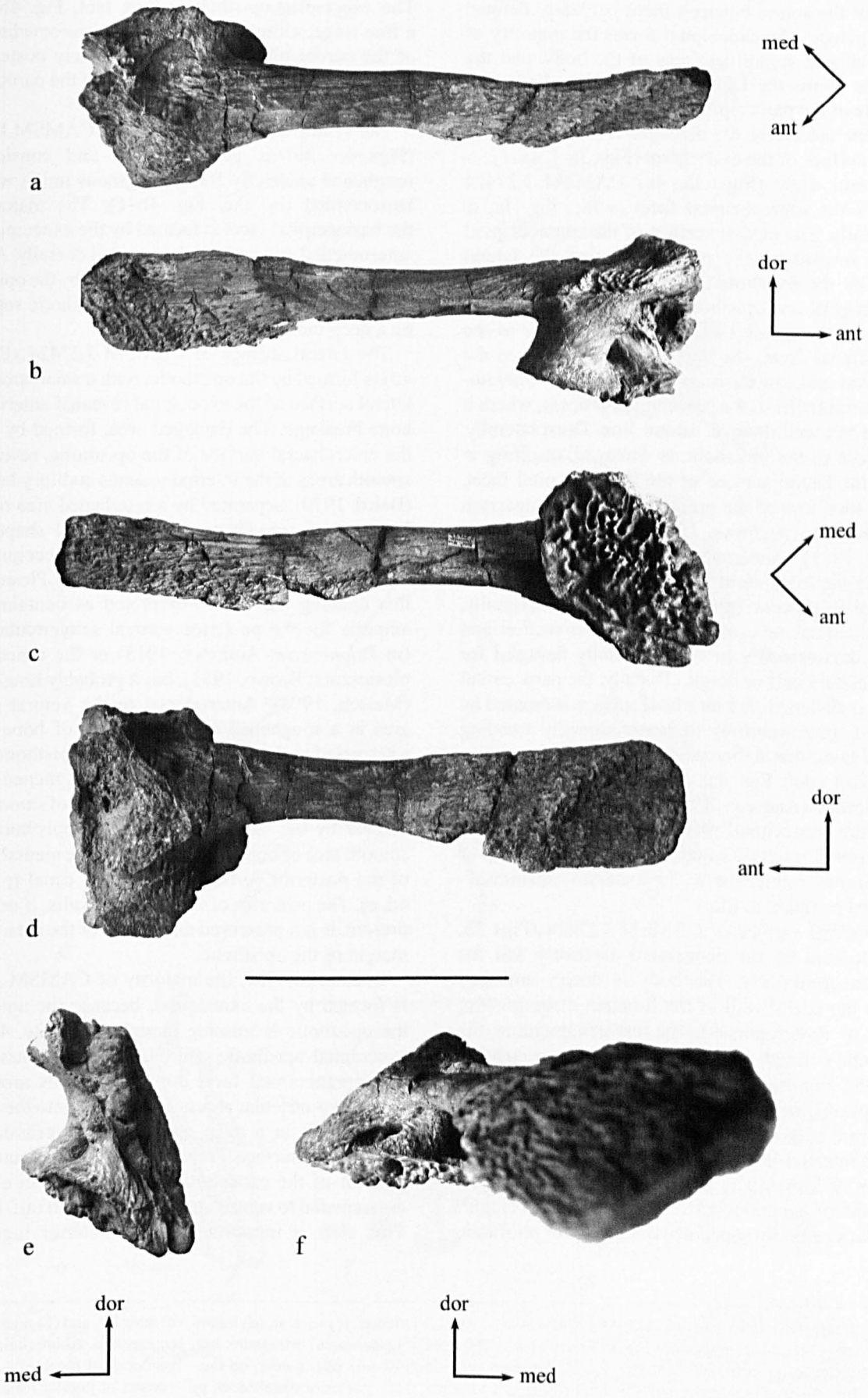

Figure 3. For legend see facing page.

fused, but the suture between them is clearly defined in most places. The exoccipital forms the majority of the medial and ventral surfaces of the body, and the opisthotic forms the lateral surface of the body and the whole of the paroccipital process. The opisthotic is incomplete anteriorly, the damaged area revealing the internal surface of the exoccipital (Figs 3a–f, 4a–f).

In dorsal view (Figs 3a, 4a) CAMSM J.27424 preserves the supraoccipital facet (s fac, Fig. 4a, d, e) anteriorly. The medial surface of the supraoccipital facet is formed by the exoccipital, and the lateral surface by the opisthotic; slight crushing has folded the exoccipital and opisthotic elements together along the line of the suture (sut, Fig. 4a). Posterior to the supraoccipital facet, the line of division between the exoccipital and opisthotic is unclear except immediately anteromedial to the paroccipital process, where it is a fine but well-defined sutural line. Dorsolaterally, the surface of the opisthotic is damaged, resulting in loss of the lateral surface of the supraoccipital facet, and the total loss of the prootic facet (by comparison to *Peloneustes* (Andrews, 1913) and *Kimmerosaurus* (Brown, 1981). Posteriorly, the opisthotic forms the whole of the long, stout and posterolaterally directed paroccipital process (pp, Fig. 4a–d, f). Proximally, the paroccipital process is oval in cross-section and slightly dorsolaterally to ventromedially flattened for approximately half its length. Distally, the paroccipital process is flattened, and its lateral surface is crossed by a curved, anteroventrally to posterodorsally trending ridge of bone that delineates the roughened posterior distal facet (pdf, Fig. 4a, d, f) for contact with the suspensorium (Andrews, 1913). The posterior terminal end of the paroccipital process (pte, Fig. 4a, c, f) is heavily pitted, strongly suggestive of a cartilage cap or dense fibrous connection to the quadrate–squamosal–pterygoid complex in life.

The medial surface of CAMSM J.27424 (Figs 3b, 4b) is formed by the exoccipital anteriorly and the opisthotic posteriorly. The body is deeply embayed to form the lateral wall of the foramen magnum (fm, Fig. 4b, e). Posterodorsal to the foramen magnum, the exoccipital is roughened into an atlas-axis articulating facet (aaf, Fig. 4a–e), equivalent to the 'facet like a zygapophysis' of *Peloneustes* (Andrews, 1913, p. 36). The ventral edge of the exoccipital gives no indication that it contacted its counterpart beneath the foramen magnum or formed any part of the occipital condyle. This lack of junction between the two exoccipital-opisthotics ventrally appears to be normal for pliosaurs. The exoccipital-opisthotic suture (sut, Fig. 4b, f) is a fine ridge, closely following the ventromedial edge of the paroccipital process. Immediately posterior of the suture, the anteromedial surface of the paroccipital process is coarsely ornamented.

The ventral surface of the body of CAMSM J.27424 (Figs 3c, 4c) is gently convex and considerably roughened anteriorly for cartilaginous union with the basioccipital (bo fac, Fig. 4b–f). The majority of the basioccipital facet is formed by the exoccipital, the anteromedial edge of which is angled dorsally. A small part of the basioccipital facet is formed by the opisthotic laterally, with the exoccipital and opisthotic separated by a deep incisure (sut, Fig. 4c).

The lateral surface of CAMSM J.27424 (Figs 3d, 4d) is formed by the opisthotic, with a small area of the lateral surface of the exoccipital revealed anteriorly by bone breakage. The damaged area, formed by loss of the anterolateral surface of the opisthotic, reveals two smooth areas of the internal osseous auditory labyrinth (Baird, 1970), separated by a roughened area of bone. The ventral smooth area is large, oval shaped, and formed by the lateral surface of the exoccipital (au, Fig. 4a, d, e). In other members of the Plesiosauria, this opening has been interpreted as containing the ampulla for the posterior vertical semicircular canal (in *Peloneustes*: Andrews, 1913) or the utriculus (in plesiosaurs: Brown, 1981), but it probably housed both (Maisch, 1998). Anterodorsal to the ventral smooth area is a roughened and pitted area of bone that is interpreted as the internal exoccipital-opisthotic suture (sut, Fig. 4c). Anterodorsal of this roughened sutural surface is a smaller, but incomplete area of smooth bone formed by the lateral surface of the opisthotic. This smooth area of bone is interpreted as the medial surface of the posterior vertical semicircular canal (pvs, Fig. 4d, e). The posterior of the fenestra ovalis, if originally present, is not preserved due to loss of the anterolateral margin of the opisthotic.

In anterior view, the majority of CAMSM J.27424 is formed by the exoccipital, because the anterior of the opisthotic is missing laterally (Figs 3e, 4e). The exoccipital-opisthotic suture (sut, Fig. 4e) passes from the supraoccipital facet dorsally, extends around the ampullary-utricular recess, and passes onto the anterior of the bone in a deep groove, before crossing onto the ventral surface. Ventromedial to the suture, the anterior of the exoccipital is pierced by an elongate, dorsomedial to ventrolateral oriented cleft (ajf, Fig. 4e). This cleft is interpreted as the anterior jugular (or

Figure 4. Interpretive drawings of CAMSM J.27424 in (a) dorsal, (b) medial, (c) ventral, (d) lateral, (e) anterior, and (f) posterolateral views; for matching photographs see Figure 3, scale bar = 100 mm; for anatomical orientation bars see Figure 3. Abbreviations: aaf – atlas-axis articulating facet, ajf – anterior jugular foramen, au – ampulla-utriculus recess, bo fac – basioccipital facet, ef – eustation foramen, fm – foramen magnum, pcf – posterior common foramen, pdf – posterior distal facet, pjf – posterior jugular foramen, pp – paroccipital process, pte – posterior terminal end, pvs – recess for posterior vertical semicircular canal, s fac – supraoccipital facet, sut – exoccipital-opisthotic suture, XII – hypoglossal foramen.

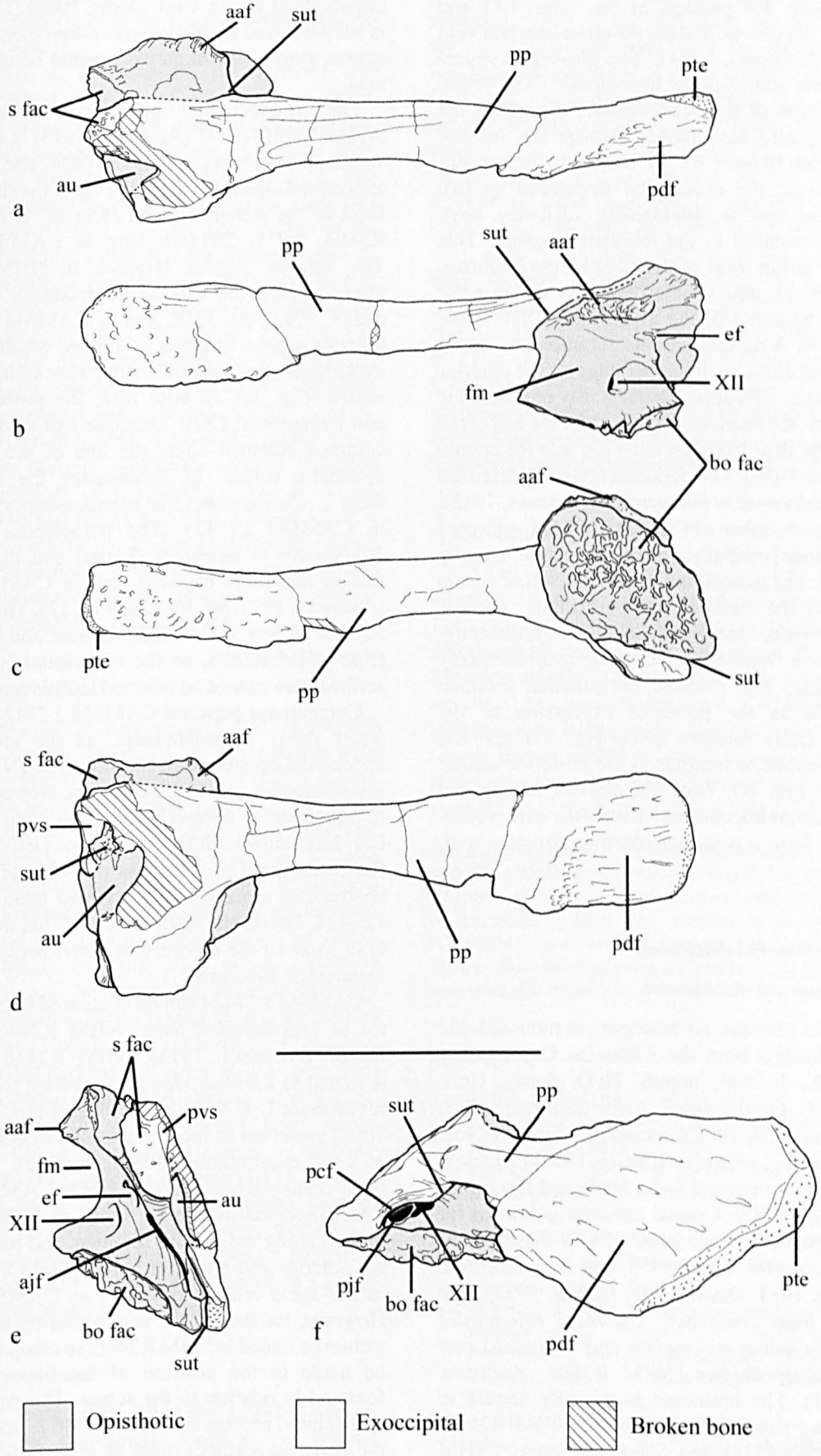

Figure 4. For legend see facing page.

vagus) foramen, for passage of the vagus (X) and accessorius (XI) nerves, and the posterior cerebral vein (Romer, 1956; Brown, 1981). The glossopharyngeal (IX) nerve, one branch of the hypoglossal (XII) nerve, and an extension of the perilymphatic duct from the inner ear may also have passed through the anterior jugular foramen (Romer, 1956). Medial to the anterior jugular foramen, the exoccipital is pierced by two foramina. The first is sub-circular, relatively large and lies anteroventral to the foramen magnum. This foramen lies at the level of the floor of the braincase (XII, Fig. 4b, e), and is interpreted as the exit for two or three branches of the hypoglossal (XII) nerve (Romer, 1956). A second, smaller foramen lies dorsal to the first and close to the upper edge of the anterior jugular foramen. This upper foramen may represent the endolymphatic foramen (ef, Fig. 4b, e) for the exit of the endolymphatic duct from the inner ear into the cranial cavity (Romer, 1956). This foramen was considered the exit for a blood vessel in *Peloneustes* (Andrews, 1913).

The posterior surface of CAMSM J.27424 is formed by the exoccipital medially, and the opisthotic laterally (Figs 3f, 4f). The exoccipital-opisthotic suture passes from beneath the base of the paroccipital process into an elongate, dorsomedially to ventrolaterally oriented groove. Within the groove lie two subequally sized foramina. The rounded dorsomedial foramen is interpreted as the posterior expression of the hypoglossal (XII) foramen (XII, Fig. 4f) and the elongate ventrolateral foramen as the posterior jugular foramen (pjf, Fig. 4f). Thus, the anterior jugular and hypoglossal foramina combine within the exoccipital-opisthotic to form a posterior common foramen (pcf, Fig. 4f).

5. Interpretation and discussion

5.a. Comparison and identification

Five species of pliosaur, all belonging to monospecific genera, are known from the Callovian Oxford Clay Formation (L. F. Noè, unpub. Ph.D. thesis, Univ. Derby, 2001): *Liopleurodon ferox* Sauvage, 1873; *Pachycostasaurus dawni* Cruickshank, Martill & Noè, 1996; *Peloneustes philarchus* (Seeley, 1869) Lydekker, 1889; *Pliosaurus andrewsi* Tarlo, 1960; and *Simolestes vorax* Andrews, 1909. Cranial material is known for all five genera (L. F. Noè, unpub. Ph.D. thesis, Univ. Derby, 2001, *contra* Tarlo, 1958; see also Andrews, 1913; Linder, 1913; Dawn, 1991; Martill, 1992). The braincase is most completely known in *Peloneustes philarchus*, including a complete and uncrushed pair of exoccipital-opisthotics (NHM R3803; Andrews, 1913, fig. 11). The braincase is partially known in *Liopleurodon ferox* (NHM R2446 and NHM R2680; Andrews, 1897, 1913) and *Simolestes vorax* (NHM R3319; Andrews, 1909, 1913), both species preserving incomplete exoccipital-opisthotic elements (L. F. Noè, unpub. Ph.D. thesis, Univ. Derby, 2001). The braincase is not preserved in *Pliosaurus andrewsi* or *Pachycostasaurus dawni*, so comparison cannot be made to these taxa.

The left exoccipital-opisthotic of *Peloneustes philarchus* NHM R3803 (Andrews, 1913) is considerably smaller than that of CAMSM J.27424. The length of the exoccipital-opisthotic from the top of the supraoccipital facet to the posterior distal facet is 78 mm in NHM R3803, but is 208 mm long in CAMSM J.27424. The anterior jugular foramen in NHM R3803 is aligned along the exoccipital-opisthotic suture (Andrews, 1913; fig. 12D), but in CAMSM J.27424 the anterior jugular foramen is situated wholly within the exoccipital, and ventral to the exoccipital-opisthotic suture (Fig. 4e). In both taxa, the posterior jugular and hypoglossal (XII) foramina exit into a posterior common foramen along the line of the exoccipital-opisthotic suture. In *Peloneustes* the basioccipital facet is sub-quadrate, but anteroposteriorly elongated in CAMSM J.27424. The paroccipital process in *Peloneustes* is relatively shorter, and the distal end thicker and more rounded than in CAMSM J.27424 (Andrews, 1913, pp. 36–7, figs 11, 12). Thus, CAMSM J.27424 differs substantially in size and morphology from NHM R3803, so the exoccipital-opisthotic described here cannot be referred to *Peloneustes*.

Comparison between CAMSM J.27424 and *Simolestes vorax* is problematic, as the surviving left exoccipital-opisthotic in the holotype (NHM R3319) is considerably crushed and broken. However, the skull of *Simolestes* is relatively short and wide (Noè, 1999; L. F. Noè, unpub. Ph.D. thesis, Univ. Derby, 2001), and the paroccipital process was probably proportionally shorter and more laterally oriented than in CAMSM J.27424. However, confirmation of this inference will have to await the recovery of better-preserved cranial material of *Simolestes*.

CAMSM J.27424 can be compared to two individuals of *Liopleurodon ferox*, NHM R2446 and NHM R2680 (Andrews, 1913). NHM R2446 (previously assigned to *Liopleurodon pachydeirus*; for taxonomic revision see L. F. Noè, unpub. Ph.D. thesis, Univ. Derby, 2001) preserves an incomplete anterior columnar body of a left exoccipital-opisthotic complex. The bone is badly damaged but of similar size to CAMSM J.27424. The exoccipital-opisthotic body of NHM R2446 is broken along the jugular foramen, and preserves both the anterior and posterior hypoglossal (XII) foramina in the same relative positions as CAMSM J.27424. However, the line of the exoccipital-opisthotic suture cannot be traced in NHM R2446, so comparison cannot be made to the position of the hypoglossal (XII) foramen in relation to the suture. The anterior of the paroccipital process of NHM R2446 is orientated with the flattened surfaces more or less vertically aligned, in contrast to the medially tilted dorsal surface of the paroccipital process in CAMSM J.27424. This

difference in orientation of the proximal end of the paroccipital process may be the result of compaction in CAMSM J.27424.

NHM R2680 is a complete, but isolated and somewhat crushed cranium of *Liopleurodon ferox*. NHM R2680 preserves a left exoccipital-opisthotic, complete with paroccipital process, which is only slightly smaller than that in CAMSM J.27424. The body is compressed between the cranial roof and palate (Andrews, 1897, 1913), and the location of the exoccipital-opisthotic suture and the various foramina cannot be determined. However, the gross morphology and relative proportions of the exoccipital-opisthotic in NHM R2680 match that of CAMSM J.27424. The distal end of the paroccipital process is somewhat thicker and more rounded in NHM R2680, although this may be a result of distortion in CAMSM J.27424. Thus, comparison of CAMSM J.27424 with the available Callovian pliosaur braincase material indicates that the morphology of CAMSM J.27424 is closest to NHM R2446 and NHM R2680. CAMSM J.27424 is therefore tentatively ascribed to *Liopleurodon ferox*. This is the first recorded occurrence of a substantially complete, three-dimensionally preserved exoccipital-opisthotic attributable to *Liopleurodon*.

5.b. The size of the animal

The size of the cranium from which CAMSM J.27424 was derived can be estimated by comparison with NHM R2680. The isolated cranium of NHM R2680 has a snout to occipital condyle length of 1120 mm (Andrews, 1913, p. 21) and a paroccipital length of 150 mm (Andrews, 1897, p. 178). CAMSM J.27424 has a paroccipital process length of 165 mm. Assuming a 1:1 growth ratio between the cranium and paroccipital process beyond the 1.12 m cranial length of NHM R2680, the length of skull from which CAMSM J.27424 came can be estimated at approximately 1.23 m. This length estimate is slightly shorter than an 'old adult' (*sensu* Brown, 1981) individual of *Liopleurodon ferox* (NHM R3536), estimated at 1265 mm from snout tip to occipital condyle (Andrews, 1913, p. 22).

The overall length of the animal from which CAMSM J.27424 came can be estimated by comparison to a skeleton of *Liopleurodon ferox* (GPIT 1754/2). GPIT 1754/2 has a skull:total body length ratio of approximately 1:5.19 (skull length 0.94 m, overall body length including skull 4.88 m). This would indicate a calculated overall body length for the CAMSM J.27424 animal of approximately 6.39 metres.

5.c. Developmental stage

A number of features of CAMSM J.27424 give an indication of the ontogenetic stage of the animal from which this element came. The exoccipital and opisthotic are fused, but this occurs early in the ontogeny of the Callovian Sauropterygia (Maisch, 1998). However, there is no indication of fusion between the exoccipital-opisthotic and the supraoccipital or basioccipital elements of the braincase. In fully adult Callovian pliosaurs, it is common for remnants of the exoccipital-opisthotic to be firmly sutured to the basioccipital (L. F. Noè, unpub. Ph.D. thesis, Univ. Derby, 2001), but the ventral surface of CAMSM J.27424 is entire and free of attached or detached bone. This precludes the individual from being an 'old adult'. However, the exoccipital-opisthotic is fully formed, with no indication of a substantial cartilaginous component. The size of CAMSM J.27424 compared to 'old adult' (*sensu* Brown, 1981) individual of *Liopleurodon ferox* (NHM R3536) also suggests CAMSM J.27424 was relatively mature. Thus, from the available evidence, the animal from which the CAMSM J.27424 was derived is inferred to have been an 'adult' individual (*sensu* Brown, 1981) at the time of death.

6. Conclusions

CAMSM J.27424 is an isolated left exoccipital-opisthotic from the braincase of a Callovian pliosaur. This exoccipital-opisthotic was recovered from the Peterborough Member or bottom of the Stewartby Member of the Oxford Clay Formation, and is attributed to *Liopleurodon ferox*. CAMSM J.27424 is interpreted as having come from an 'adult' individual (*sensu* Brown, 1981) of *Liopleurodon* with a cranial length of approximately 1.23 metres and an estimated overall body length of approximately 6.39 metres.

Acknowledgements. We would like to thank David Norman and Mike Dorling (CAMSM), Angela Milner and Sandra Chapman (NHM), for their assistance and providing access to specimens in their care. Comments by David Norman (CAMSM), Don Smith (University of Derby) and Mike Taylor (National Museums of Scotland) have substantially improved this manuscript.

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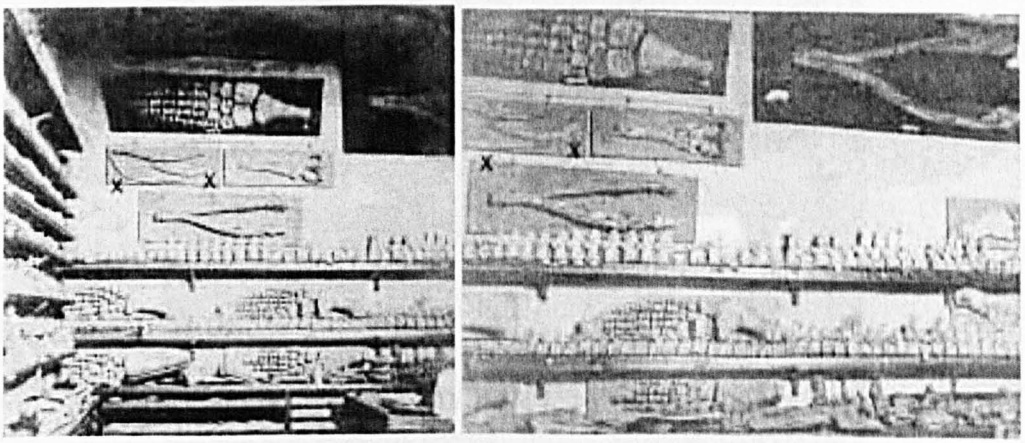
Appendix IX

COMMENTARY ON COLLECTIONS: NOTES ON THE HYPODIGM OF SPECIMENS REFERRED TO *LEEDSICHTHYS*.

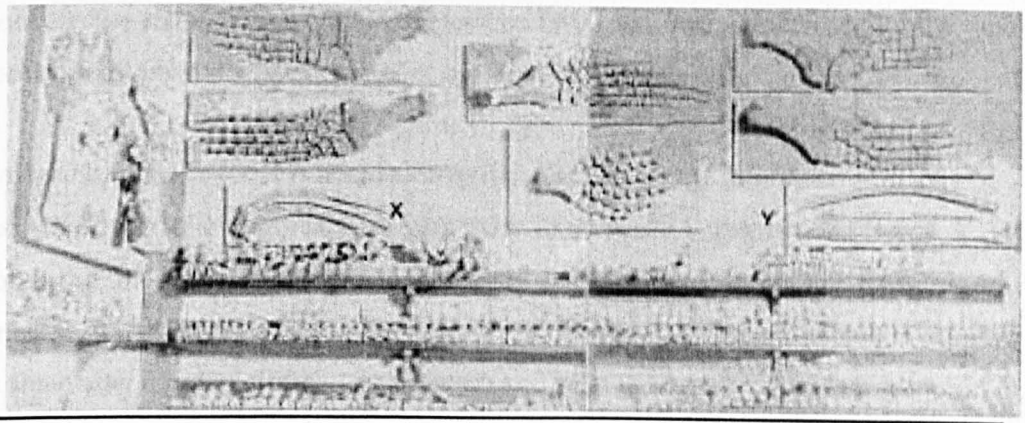
Natural History Museum (London)

The most challenging of all the collections of *Leedsichthys* material to interpret is that of the NHM (London) – less because of it containing type material, more because of the severe mixing that it has been subjected to over time.

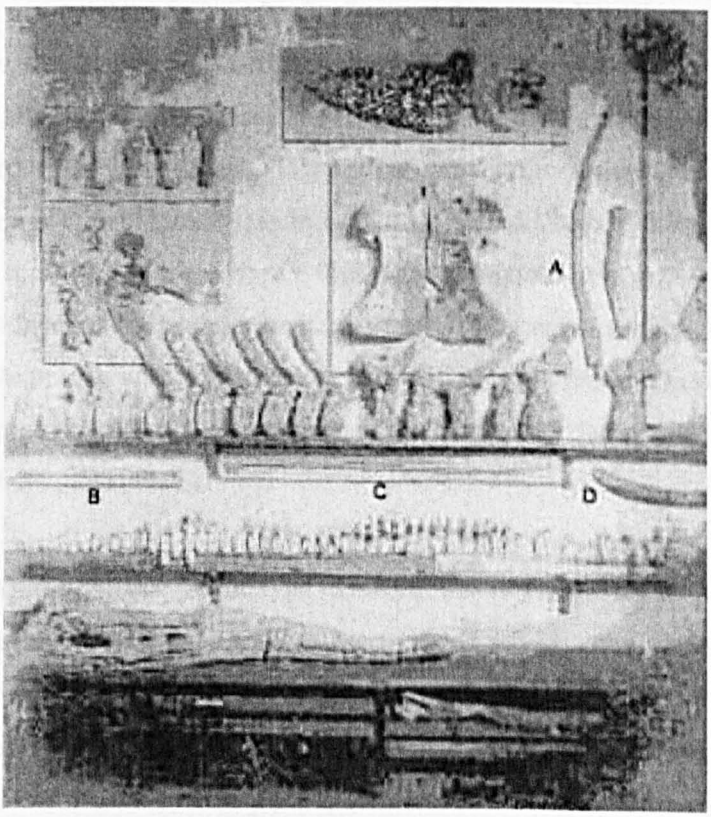
Mixing is virtually inevitable when specimens are moved, whether from pit to home, home to museum store, museum store to new building. What is most frustrating about this material, is that we have glimpses of it very early on, even before it is described in print. There are photographs of the disposition of Alfred Leeds' Eyebury 'Bone Room' attics both before (fig.1) and after (fig.2,3) the 'First Collection' was sold to the British Museum (Natural History). Thus, elements currently numbered as part of BMNH P.6925 are visible on the wall prior to the First Collection sale, specimen BMNH P.11826 can be seen on the west wall of the large attic in 1890-1892, and other as yet unidentified (possibly purchased by Stürtz of Bonn) *Leedsichthys* bones can be seen to the left and above the pliosaur rib GLAHM V.1374 sold to the Hunterian Museum 1915-1919.



Appendix IX Figure 1: The south east corner (left) and the south wall (right) of the large attic 'bone room' at Eyebury, before the sale of the 'First Collection'. Two identified elements from BMNH P.6925 lie adjacent to the letter 'X'.



Appendix IX Figure 2: The west wall (right) of the large attic 'bone room' at Eyebury, after the sale of the 'First Collection'. Specimen BMNH P.11826 lies to the left of the letter 'X'. The *Leedsichthys* specimens to the right of the letter 'Y' are yet to be identified.



Appendix IX Figure 3: The south wall of the large attic 'bone room' at Eyebury, after the sale of the 'First Collection'. Stegosaur vertebrae constrain the date to probably between 1898 and 1904. Unidentified *Leedsichthys* specimens are marked A, B and C, near the Hunterian Museum pliosaur rib GLAHM V1374 marked by the letter 'D'.

Of the 23 specimens of this taxon currently held by the NHM (London), only 3 are not collected by Alfred Leeds. Of the 20, 10 specimens (P.6921-P.6930 inclusive) were part of the 'First Collection' sold by Alfred to the BM, after the wealth of his collection was

discovered by Henry Woodward in September 1885, and the material used for the type description is drawn from this series of specimens.

The *Leedsichthys* material is noted as arriving at the BM(NH) in May 1892, and is accessioned the following year. Of even more importance, is the fact that Henry Woodward filled a notebook with his astonished observations during that first visit to Eyebury. According to this document, the *Leedsichthys* material was stored in drawers in the small attic room in cabinets on the north and west walls. The notebook is so meticulously detailled, with type and numbers of different bony elements and occasional measurements, that from his descriptions of the contents of various drawers one can interpret which particular specimen of *Leedsichthys* within the NHM (London) today that he is referring to (e.g. "Head bones of a very huge undescribed bony fish." and "9 large rib-like Fish- bones perhaps Gyrosteus? (2ft. Long)" in the north cabinet both appear to be distinctive parts of BMNH P.6921, whereas "huge fish coracoid 2'.7" long" in the second drawer of the west wall appears to be BMNH P.6922). "Large flat plates (Fish?) 1'.8" x 1.0"[50cm x 30cm]" is likely to be one of the two plates referred to by Hulke (1887) and Smith Woodward in 1889 – although Hulke did record a larger bone of this type with around 80cm measurement, which may indicate that Alfred Leeds managed to restore more of the specimen after Henry Woodward's visit, which may not have remained intact by the time Smith Woodward came to describe it. Certainly, as noted in section 8.3.1.1, today neither of the two plates can be reconstructed beyond 45cm in maximum dimension, although there are many unlocated fragments with these bones that might, with no little patience, extend the plates further.

Such points are of importance, as the type description is not restricted to one specimen. The lump of gill-rakers from the Vaches Noire (BMNH 32581, acquired by Richard Owen from Tesson of Caen in 1857) is specifically cited at the end of the description, but the elements forming the bulk of the description do not appear to have received accession or catalogue numbers at the time of the description, so one is reliant on the red markers applied to the bones to indicate which ones are used in the description. The result of this is that it is indicated that specimens P.6921, P.6922 and P.6925 are all used. This is interesting, as P.6922 (the preopercle) is referred to as being "doubtfully" part of the series of bones being described. One cannot but help speculate on what can create 'doubt', where there appears to have been some tenuous possibility of the two specimens being part of the same individual. Because Smith Woodward indicates that P.6922 cannot be definitely excluded from the individual represented by BMNH P.6921, it seems that his

doubt most probably arises from its degree of physical separation from the rest of the material. From our current standpoint, we can look back with a little more wisdom on the remains that Smith Woodward tentatively described, based on the much larger (and more extensive) number of specimens known. Smith Woodward thought that he was dealing with a sturgeon-like fish, something like *Chondrosteus*, and misidentified the hypobranchial as the hyomandibula – a misidentification that reveals an incorrectly low estimation of the size of the animal and the extent which its body should cover. Today, we know that this animal is likely to have grown in excess of 9 metres, with significant gaps between bony elements of its skeleton. We also know that the remains of *Leedsichthys* can cover a considerably different area, and be separated by gaps where the unossified axial skeleton simply does not preserve – although his constrained specimen "was spread over an area of probably not less than twelve square yards [or between 3 and 3.5m^2]", the Star Pit specimen ('Ariston') excavated during the field seasons of 2002 and 2003 was spread over a core area of 72m^2, with oher elements found a further twelve metres away. If Smith Woodward was being conservative on the basis of gaps and sizes, his statement of "doubtfully forming part of the series", implies that P.6922 was found near to the main collection of P.6921 material with no real difference in the stratigraphic level at which it was found.

Setting aside P.6922, what of the others in the series, namely P.6923-P.6930 – is there any possibility that they are part of the same individual? The only way to determine that involves a careful examination of the many hundreds of fragments that make up each specimen.

Why are there are so many fragments in these specimens – especially when the original accession register records "around 180 bones" for all ten specimens? Part of the reason is that during a collection move from the basement of the main BM(NH) building to the new palaeontology annexe, a flatbed trolley carrying the bulk of the instituion's holdings of *Leedsichthys* was unbalanced when moving to the fossil fish level from the lift (the lift does not stop at exactly the correct altitude for a smooth transition to the floor) in January 1972. Evidence of this disaster is scattered through the specimens – careful examination reveals elements of other specimens distributed through most drawers: part of P.6921 is contained within P.11823; P.6930 contains parts of P.6927, P.6926 and P.6925; P6925 has parts of P.6928; P.11823 has part of P.10000.

But this does not particularly help us with the question of how associated these specimens actually were – many of these fragments are unnumbered, so it is not clear which specimen is the correct 'home' of the fragments: an unnumbered piece in P.6927 connects to an unnumbered fragment in P.6925. These unnumbered fragments could easily have been misassociated during the overturning of the flatbed trolley: only when one gets two elements with numbers (which were applied prior to the 1972 move) on them that are different, yet are in some unquestionable way related, can one start to argue a broader association. Interestingly, there are such elements.

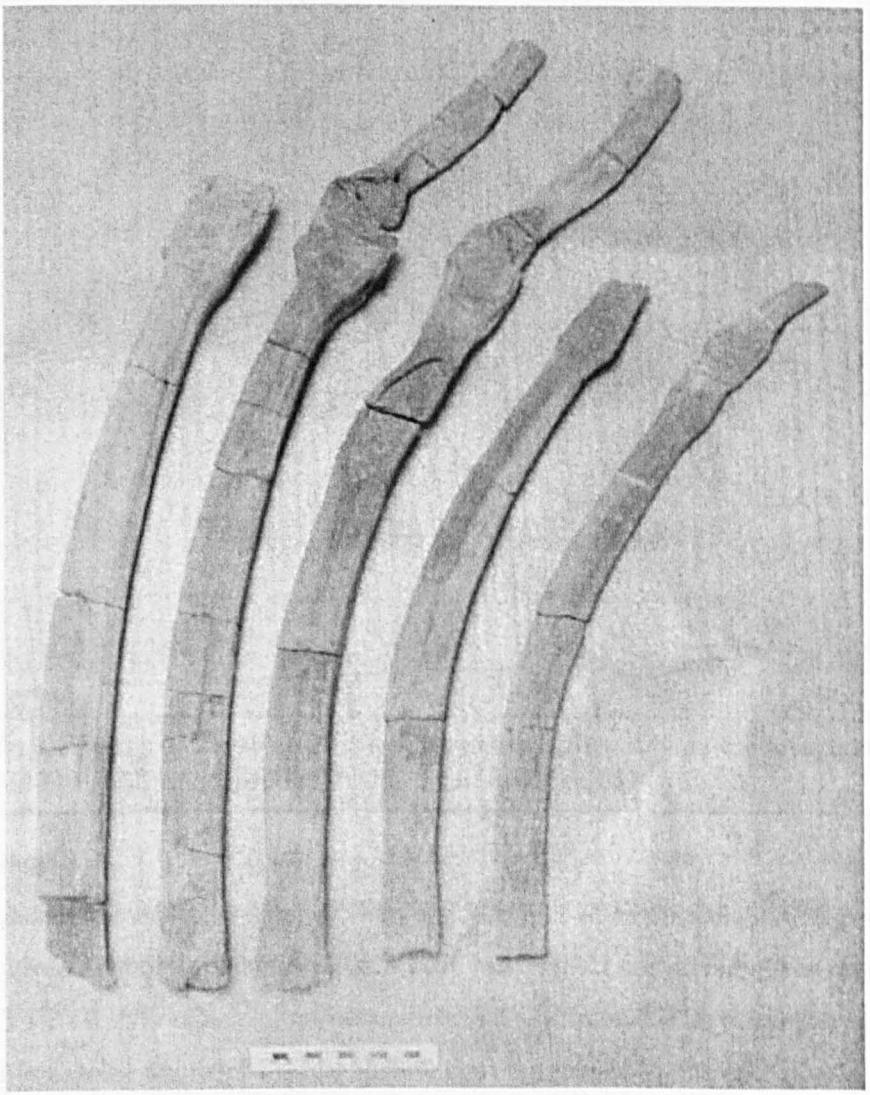
P.6924, as noted in section 9.3.3.7, is a series of dorsal fin spines with an extremely unusual pattern of healed bone calluses, probably representing an unsuccessful pliosaur attack. Placing the bones together in an *in vivo* position reveals what appears to be a bite pattern (fig.9.3a-c). Within P.6925 is a numbered dorsal fin spine (fig. 4) with a very similar pattern of preservation, and the same highly unusual pathology. It can be placed in sequence with the bones of P.6924 as part of the bite pattern.

Even more convincing are two fragments, one numbered P.6925, and one numbered P.6928. Two parts of a large elongate element (fig. 5), they were clearly broken (and most likely separated) prior to burial – their edges are worn and rounded, but have a unique stepped fracture pattern in the periosteum which can been matched between both fragments (fig. 6).

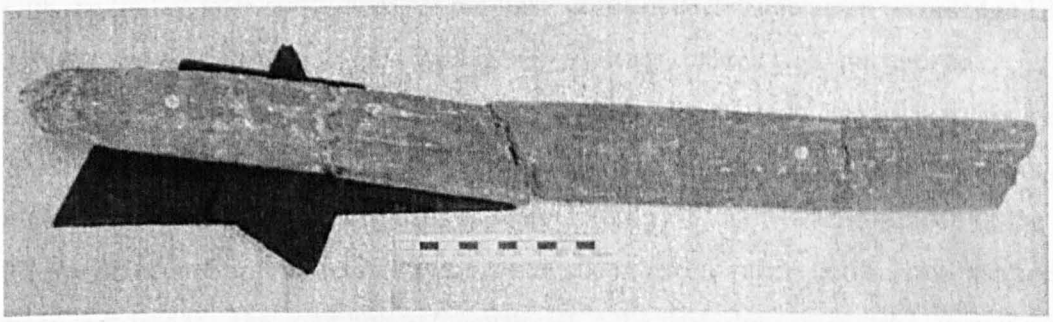
Of course, this cannot prove that all elements of these specimens belong to the same individual – but they do indicate a degree of overlap between the specimens, which might be interpreted as constraining how far apart they were found.

Beyond these initial findings (and such they must be referred to, as the process of assessing all specimens involved in the 'capsizing flatbed trolley' involves literally thousands of fragments and sadly lies outwith the immediate focus of this project – perhaps constituting a Masters project of its own), it can be observed that looking through the series P.6921-P.6930 after a protracted series of repairs there are a numbers of clusters of elements whose osteological (e.g. caudal fin ray fragment) or preservational natures would seem to indicate that they are associated with the 'wrong' specimen number, and an attempt to find joins between such fragments and their suspected 'host' specimen would no doubt yield positive results.

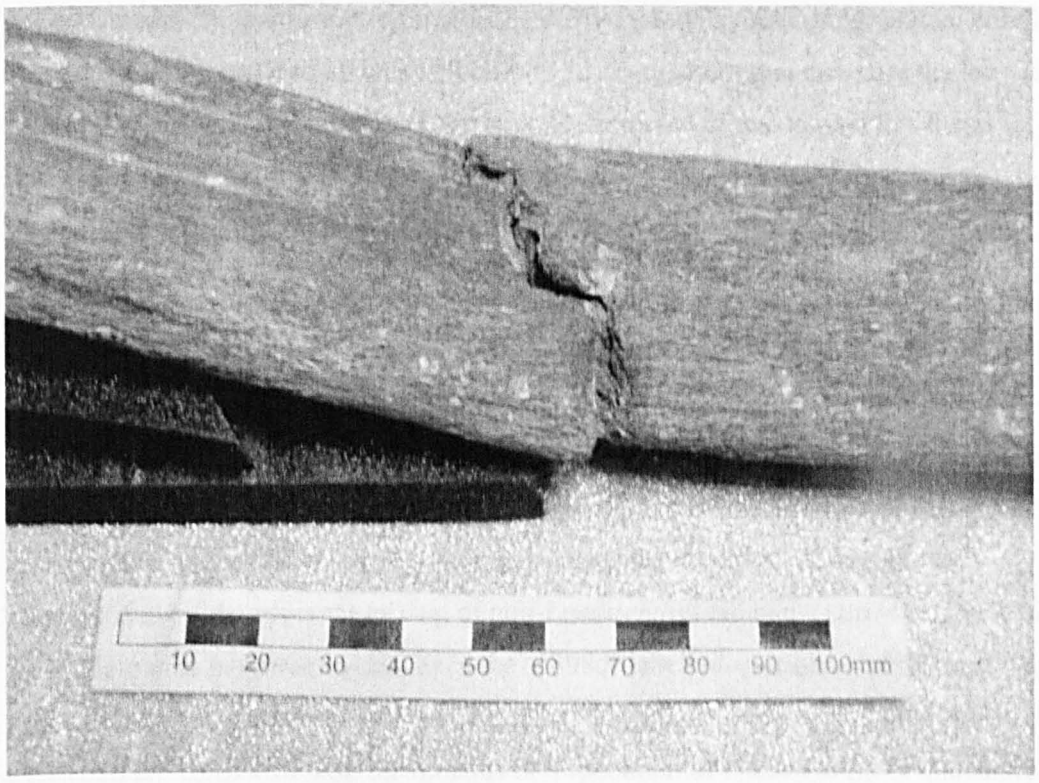
This would seem a worthwhile step in restoring the specimens damaged in the flatbed trolley incident, and so aiding a more full understanding of the original 'type series'.



Appendix IX Figure 4: Four 'dorsal fin spines' of BMNH P.6924 lie adjacent to (left) a numbered identical element from BMNH P.6925. All elements share a common preservation with a highly unusual callus growth of bone at a matching point in the bone. Scale is 100mm.



Appendix IX Figure 5: Numbered specimens from BMNH P.6928 (left) and BMNH P.6925 (right), showing their common break surface. Scale is 100mm.



Appendix IX Figure 6: Close-up of matching join surfaces of numbered fragments from BMNH P.6928 and BMNH P.6925. Scale is 100mm.

Other questions:

The specimen depicted in the letter of 1894 (fig. 8.10b) and its possible indication of a misassociation of a bony concretion (fig. 8.10a) with P.6921 has already been referred to in section 8.3.1.7. It only remains to reiterate that that specimen has no catalogue number on it at all (although the number '4' is on a white square attached to one of the curving components), therefore could easily have been placed with P.6921 by accident in the wake of the trolley capsizing in January 1972.

BMNH P.10000, or the 'Tail specimen', has a more chequered and hazy curatorial record, with the trail of false attributions for the 'rest' of the collected specimen recorded in Liston & Noè 2004 (see Chapter 3), and leading subsequently to three large drawers of unnumbered fragments, one of which bore a tin with Alfred Leeds' handwriting upon it. These three drawers (resembling large laptop tables in design) are a form found in only one other place in the fossil fish department of the Natural History Museum (London): the drawer that contains the pectoral fin fragment and other gill rakers and fin rays marked BMNH P.10000. The condition of the material in the three drawers matches that of the material in the fourth drawer exactly: highly pyritic, dark brown, brittle, and completely unlike any other specimen of *Leedsichthys*. The material also consists of skull material: the only part of the tail specimen sold to the BM(NH) that was still untraced. The

combination of unique furniture for storage, Alfred Leeds' handwriting, unique condition and colour of the material all makes for a powerful argument that these are the long lost elements of the tail specimen, and they have been treated in that way in this thesis.

Sedgwick Museum, University of Cambridge

Doubt over identifications and separation of pieces over time has resulted in the sundering of relationships between objects – the only associated sequence that still survives is the series marked '1898d' (J.67413-J.67470), which is noted as associated and stored in 3 trays. However J.67413-J.67440 are the only items bearing the 1898d labels, so some doubt must arise over the relatedness of J.67441-J.67470 (both in terms of being part of the same animal, as well as of whether they have the same context). This doubt is compounded by the apparent mixing of non-*Leedsichthys* elements (J.67413, J.67416, J.67422, to note but three) within even the '1898d' labelled specimens of this associated series. However, the majority of the pieces in this series (including the unlabelled elements) are consistent with the remains of a specimen of *Leedsichthys* of unusually small size.

Other specimens, which have broken, or separated from their original number in some way, have been retrospectively reunited by determining common join surfaces between fragments. In particular, there are six fin lobes within the Sedgwick collections, whose true scale (with display in mind) has been forgotten: one is a pectoral fin section around 60cm long, constituted by J.67483+J.66922+J.66929+J.66920 (erroneously given a modern label with Fletton 1899 on it) +4 unnumbered fragments, from "H.K. 1900 Fletton"; the other five are sections of probable caudal lobes. The first is solely represented by J.66944. The second is represented by Bertie Brighton's "cannot now remember" specimen (X.39250, formerly referred to as 'the sweepings' specimen, for obvious reasons, as it decayed on display) and X.50125/LP.17. The third is made up of J.66924+J.66937 (also "H.K. 1900 Fletton"). The fourth is J.66936+J.66939+J.66941+J.66921 ("Fletton 1899"). The fifth (again, "H.K. 1900 Fletton") consists of J.66925+J.66926+J.66940+J.66935.

Some specimens remain unnumbered (in LP drawer, plus two glass cases of flat triangular bones – unlikely to be scales given the recognised form of pachycormid scale, and the trend of decreasing ossification of scales with increasing adult size in pachycormids, but highly unusual if they are sclerotic ring scales).

A final anomaly is V.787 – although it came with the Sedgwick material, it appears at odds with their prefix systems old and new.

Hunterian Museum, University of Glasgow

The Hunterian's holdings – bar recent acquisitions of thin-sections and casts related to this project – have consisted of two specimens: GLAHM V3362 the branching caudal fin-ray (fig. 8.42b) and GLAHM V3363 – 'Big Meg'. Although 'Big Meg' had the reputation of the most complete specimen in museum collections, acquired as a series from Alfred Leeds in the first half of 1915, a doubt has arisen regarding how extensive this specimen originally was when first purchased from.

The original sales receipt (dated 18th June 1915) lists the following items, as a batch for £5: 'Leedsia probl. 5 trays of skull bones; 2 trays of ribs; 2 fitting bones; 1 strand of tail; 1 gill raker; & flat bone (clavicle?)'. The strand of tail is accessioned as GLAHM V3362, and a number of these elements are identifiable today.

This doubt about whether this specimen has been 'added to', has origins in the packing list of the crates used to transport the 'Second Collection' to the Hunterian Museum two years after Alfred Leeds' death, in 1919. The crate listings were compiled by CJ Gregory and WR Smellie while they packed the collection between 27/8 and 2/9/1919. Although they are sometimes vague, and generally consist of ichthyosaurs, plesiosaurs and marine crocodiles (in a way that reflects the general abundance of the different taxa in the clay), a line in the packing list for crate 112, which notes the presence of *Cryptoclidus* coracoids and pliosaur ribs and paddles, says the word 'Leedsia'. This indicates that *Leedsichthys* was indeed part of this final shipment from Eyebury. Although it does not appear to be a large part of the shipment, and is not likely to constitute a significant percentage of today's GLAHM V3363, it is undeniably present, and these elements are likely to have been unknowingly 'added into' V3363 when the crates were discovered in the 1960s by new members of staff. This also might explain the high quantity of some bone types present (anal fin supports and robust curved elements in particular, see Table, but also 2 gill rakers, instead of the one listed above).

A good deal of V3363 can be identified as being part of the original purchase, as Alfred Leeds recorded in an accompanying dated (January 1915) note that the bones are numbered and fragments making one bone are wrapped together. The numbers are still applied to many of the bones today, as are notes indicating if they are 'paired'.

Original numbers on some specimens that date from before the Second World War serve to distinguish original bones from possible 'late arrivals'. Further work is planned to constrain which elements are properly numbered and/or described as being present, and which might have come subsequently to the collection. A review of the elements that make up this specimen, based on these original numbers and the numbers applied by Alfred Leeds, would reveal which were definitely part of the 1915 purchase, and which are possible 'post-war additions'.

New Walk Museum, Leicester City Council

Historically, this collection has been subjected to many reorganisations. Changes in procedures for numbering meant that specimens were often renumbered, with an increasingly detailed taxonomic-based prefix system requiring progressive reformatting of numbers (and consequent alteration of duplicate numbers often created by that process). However, this does not cause a particularly insurmountable problem for the *Leedsichthys* material from this collection. The largest obstacle to identification of specific items accessioned is the apparent refusal to apply numbers or labels to the specimens – the only exception to this being specimens that arrived from Peterborough Museum in the 1950s. Many specimens are mounted on boards – but the wording on the boards is usually sufficiently different to the wording in the accession registers as to prevent confident association of an accession number with a particular mounted specimen (conflicting statements include 'donated' as against 'purchased' and 'reptile' instead of 'acipenseroid fish').

As with other institutions, the lack of interest in this taxon from external researchers has undoubtedly compounded the problem and allowed this section of the collection to languish in the absence of published literature for curators to refer to for anything other than the woolliest osteological identifications. Researchers cannot complain that the specimens they wish to work on are not well-identified, if the work to identify them has not been published in the literature for the curators to use. What is presented here is the best determination possible given descriptions in registers, descriptions on display boards and apparent similarities in material. The New Walk collections contain some particularly important pieces, so the limitations of the associated contextual information is particularly frustrating. However, the degree to which useful information on geological rather than historical context would be forthcoming is severely limited: the information provided by collectors is seldom other than 'Oxford Clay of Peterborough'.

Appendix IX Table 1a. Details of *Leedsichthys* specimens in Sedgwick Museum collections.

ACCESSION NO.	COLLECTOR	DATE	LOCALITY	DESCRIPTION
CAMSM J.27416	[unknown]	1899	Fletton [Huntingdonshire]	hypobranchial
CAMSM J.27417	[unknown]	1899	Fletton [Huntingdonshire]	?hypobranchial
CAMSM J.27418	[unknown]	1899	Fletton [Huntingdonshire]	partial callus formation
CAMSM J.27419	[unknown]	1899	Fletton [Huntingdonshire]	partial callus formation
CAMSM J.27420		1901	Fletton [Huntingdonshire]	preopercular ridge fragment
CAMSM J.27421		1901	Fletton [Huntingdonshire]	possible dorsal fin spine tip
CAMSM J.27422		1901	Fletton [Huntingdonshire]	possible dorsal fin spine tip
CAMSM J.27423		1901	Fletton [Huntingdonshire]	possible dorsal fin spine tip
CAMSM J.27424				PLIOSAUR EXOCCIPITAL-OPISTHOTIC
CAMSM J.27425	?	?	Whittlesea	odd 'junction' bone - tip of a lepidotrichium? Like J.67424
CAMSM J.27426	Henry Keeping	1898	[Fletton, Northamptonshire]	pectoral fin ray fragment
CAMSM J.27427	Henry Keeping	1898	[Fletton, Northamptonshire]	pectoral fin ray fragment
CAMSM J.27428	Henry Keeping	1898	[Fletton, Northamptonshire]	pectoral fin ray fragmentt - links to J.27433
CAMSM J.27429	Henry Keeping	1898	[Fletton, Northamptonshire]	pectoral fin ray fragment
CAMSM J.27430	Henry Keeping	1898	[Fletton, Northamptonshire]	pectoral fin ray fragment
CAMSM J.27431	Henry Keeping	1898	[Fletton, Northamptonshire]	pectoral fin ray fragment (2)
CAMSM J.27432	Henry Keeping	1898	[Fletton, Northamptonshire]	pectoral fin ray fragment

CAMSM J.27433	Henry Keeping	1898 [Fletton, Northamptonshire]	pectoral fin ray fragmentt - links to J.27428
CAMSM J.27434	Alfred Nicholson Leeds	? [Fletton, Northamptonshire]	?juvenile hypobranchial?
CAMSM J.27435	Alfred Nicholson Leeds	? [Fletton, Northamptonshire]	unident. frag. (1)
CAMSM J.27436	Alfred Nicholson Leeds	? [Fletton, Northamptonshire]	unident. frag. (1)
CAMSM J.27437	Alfred Nicholson Leeds	? [Fletton, Northamptonshire]	possible propercular fragment (1)
CAMSM J.27438	Alfred Nicholson Leeds	? [Fletton, Northamptonshire]	hypobranchial (1)
CAMSM J.27439	Alfred Nicholson Leeds	? [Fletton, Northamptonshire]	proximal radial (1)
CAMSM J.27440	Alfred Nicholson Leeds	? [Fletton, Northamptonshire]	dorsal fin spine (1)
CAMSM J.27441	Alfred Nicholson Leeds	? [Fletton, Northamptonshire]	proximal radial (1)
CAMSM J.27442	Alfred Nicholson Leeds	? [Fletton, Northamptonshire]	proximal radial (1)
CAMSM J.27443	Alfred Nicholson Leeds	? [Fletton, Northamptonshire]	dorsal fin spine (1)
CAMSM J.27444	Alfred Nicholson Leeds	? [Fletton, Northamptonshire]	dorsal fin spine or curved element, possible tooth mark
CAMSM J.27445	Alfred Nicholson Leeds	? [Fletton, Northamptonshire]	bifurcating fin ray (4)
CAMSM J.35320	?	? [Fletton, Northamptonshire]	connects to X.50124/LP.15 - left parietal with ceratobranchial and mass of gill rakers ("showing hooks on 'branchiostegal'")
CAMSM J.46873	Henry Keeping	1899 [Fletton, Northamptonshire]	dorsal fin ray series (figured by von Huene) including dorsal 'support'?, a-right hyomandibula
CAMSM J.46874	Henry Keeping	1898 [Fletton, Northamptonshire]	stegosaur armour (figured by HG Seeley)
CAMSM J.46875			UNSEEN
CAMSM J.46876		1899 Fletton [Huntingdonshire]	dorsal fin spine

CAMSM J.46877		1902	Whittlesea	dorsal fin spine
CAMSM J.46878		1902	Whittlesea	dorsal fin spine
CAMSM J.46879	Henry Keeping	1902	Whittlesea	stegosaur tail spine
CAMSM J.66124			Whittlesea	J.66124/6/7/8 all join to make root of caudal ray like V3362 ("plesiosaurian")
CAMSM J.66126			Whittlesea	J.66124/6/7/8 all join to make root of caudal ray like V3362 ("?crocodilian")
CAMSM J.66127			Whittlesea	J.66124/6/7/8 all join to make root of caudal ray like V3362 ("?crocodilian")
CAMSM J.66128			Whittlesea	J.66124/6/7/8 all join to make root of caudal ray like V3362 ("?crocodilian")
CAMSM J.66920	Henry Keeping ('H.K.')	1900	Fletton [Huntingdonshire]	pectoral fragment
CAMSM J.66921	?	1899	Fletton [Huntingdonshire]	probable caudal fragment
CAMSM J.66922	Henry Keeping ('H.K.')	1900	Fletton [Huntingdonshire]	pectoral fragment
CAMSM J.66923	Henry Keeping ('H.K.')	1900	Fletton [Huntingdonshire]	distal end of preopercle
CAMSM J.66924	Henry Keeping ('H.K.')	1900	Fletton [Huntingdonshire]	probable caudal fragment
CAMSM J.66925	Henry Keeping ('H.K.')	1900	Fletton [Huntingdonshire]	probable caudal fragment
CAMSM J.66926	Henry Keeping ('H.K.')	1900	Fletton [Huntingdonshire]	probable caudal fragment
CAMSM J.66927	?	?	?	parts of two adjacent ceratobranchials
CAMSM J.66928	Henry Keeping ('H.K.')	1900	Fletton [Huntingdonshire]	two hypobranchials
CAMSM J.66929	Henry Keeping ('H.K.')	1900	Fletton [Huntingdonshire]	pectoral fragment
CAMSM J.66930	Henry Keeping ('H.K.')	1900	[Fletton, Northamptonshire]	two hypobranchials
CAMSM J.66931	?	1900	[Fletton, Northamptonshire]	mass of gill rakers
CAMSM J.66932	?	1900	[Fletton,	mass of gill rakers

			Northamptonshire]	
CAMSM J.66933	Henry Keeping ('H.K.')	1900	[Fletton, Northamptonshire]	ceratobranchial fragment
CAMSM J.66935	Henry Keeping ('H.K.')	1900	Fletton [Huntingdonshire]	probable caudal fragment
CAMSM J.66936	?	1899	Fletton [Huntingdonshire]	probable caudal fragment
CAMSM J.66937	Henry Keeping ('H.K.')	1900	Fletton [Huntingdonshire]	probable caudal fragment
CAMSM J.66938	?	1898d	Fletton [Huntingdonshire]	bone fragments - ?left preopercle, 593mm long
CAMSM J.66939	?	?	Fletton [Huntingdonshire]	probable caudal fragment
CAMSM J.66940	Henry Keeping ('H.K.')	1900	Fletton [Huntingdonshire]	probable caudal fragment
CAMSM J.66941	?	?	Fletton [Huntingdonshire]	probable caudal fragment
CAMSM J.66942	?	?	[Fletton, Northamptonshire]	J.66942 glued to J.66943 - ceratobranchial termination
CAMSM J.66943	?	?	[Fletton, Northamptonshire]	J.66942 glued to J.66943 - ceratobranchial termination
CAMSM J.66944	?	?	[Fletton, Northamptonshire]	tip of probable caudal fragment
CAMSM J.67413	?	1898d	Fletton [Huntingdonshire]	unident. frag. (resemblance to ophthalmosaur prefrontal/postorbital)
CAMSM J.67414	?	1898d	Fletton [Huntingdonshire]	proximal end of dorsal fin spine
CAMSM J.67415	?	1898d	Fletton [Huntingdonshire]	radiale fragment
CAMSM J.67416	?	1898d	Fletton [Huntingdonshire]	strongly curved element (like eg V3363, but much smaller) although passing resemblance to ophthalmosaur left clavicle
CAMSM J.67417	?	1898d	Fletton [Huntingdonshire]	small 'starred' bone like Cambridge V.787
CAMSM J.67418	?	1898d	Fletton [Huntingdonshire]	radiale fragment

CAMSM J.67419	?	1898d Fletton [Huntingdonshire]	large circular articular surface - unident. - resembles 'joint' of Butterfly bone
CAMSM J.67420	?	1898d Fletton [Huntingdonshire]	bone fragments - right parietal (juvenile)
CAMSM J.67421	?	1898d Fletton [Huntingdonshire]	distal part of preopercle or Butterfly bone
CAMSM J.67422	?	1898d Fletton [Huntingdonshire]	strong resemblance to GLAHM ?gastralium (possibly pathological - NOT V1688)
CAMSM J.67423	?	1898d Fletton [Huntingdonshire]	dorsal fin spine element, possibly with flattened callus/joint
CAMSM J.67424	?	1898d Fletton [Huntingdonshire]	circular articular surface, like J.27425, possible teeth fragments embedded in it
CAMSM J.67425	?	1898d Fletton [Huntingdonshire]	proximal radial fragment
CAMSM J.67426	?	1898d Fletton [Huntingdonshire]	distal end of dorsal fin spine
CAMSM J.67427	?	1898d Fletton [Huntingdonshire]	possible dorsal fin spine, but severely damaged
CAMSM J.67428	?	1898d Fletton [Huntingdonshire]	possible dorsal fin spine, but severely damaged
CAMSM J.67429	?	1898d Fletton [Huntingdonshire]	character of pectoral fin, possibly near base
CAMSM J.67430	?	? [Fletton, Northamptonshire]	as J.67423
CAMSM J.67431	?	? [Fletton, Northamptonshire]	?hypobranchial
CAMSM J.67432	?	1898d Fletton [Huntingdonshire]	as J.67423
CAMSM J.67433	?	? [Fletton, Northamptonshire]	base of dorsal fin spine
CAMSM J.67434	?	? [Fletton, Northamptonshire]	distal fragment of anal fin support
CAMSM J.67435	?	? [Fletton, Northamptonshire]	as J.27425
CAMSM J.67436	?	? [Fletton, Northamptonshire]	possible pectoral-related element

CAMSM J.67437	?	1898d	Fletton [Huntingdonshire]	inferior end of left cleithrum (see F.174/10,004)
CAMSM J.67438	?	1898d	Fletton [Huntingdonshire]	possible distal end of left parietal (see J.67420 and P.6921)
CAMSM J.67439	?	1898d	Fletton [Huntingdonshire]	unident. frag.
CAMSM J.67440	?	1898d	Fletton [Huntingdonshire]	elongate element, possibly dorsal fin spine
CAMSM J.67441	?	?	[Fletton, Northamptonshire]	striated caudal ray
CAMSM J.67442	?	?	[Fletton, Northamptonshire]	striated and bifurcating caudal ray with possible breaks callus/joints
CAMSM J.67443	?	?	[Fletton, Northamptonshire]	striated caudal ray with flattened end
CAMSM J.67444	?	?	[Fletton, Northamptonshire]	striated caudal ray (possibly bifurcating) with possible break callus/joint
CAMSM J.67445	?	?	[Fletton, Northamptonshire]	striated caudal ray bifurcating with possible break callus/joint
CAMSM J.67446	?	?	[Fletton, Northamptonshire]	striated caudal ray, possibly broken through callus
CAMSM J.67447	?	?	[Fletton, Northamptonshire]	striated caudal ray, possibly broken through callus
CAMSM J.67448	?	?	[Fletton, Northamptonshire]	striated caudal ray with flattened end
CAMSM J.67449	?	?	[Fletton, Northamptonshire]	striated caudal ray with flattened end
CAMSM J.67450	?	?	[Fletton, Northamptonshire]	distal tail ray fragment (just after bifurcation point)
CAMSM J.67451	?	?	[Fletton, Northamptonshire]	bifurcating distal caudal ray, one hemitrichium missing (segment?)
CAMSM J.67452	?	?	[Fletton, Northamptonshire]	striated caudal ray with flattened end
CAMSM J.67453	?	?	[Fletton, Northamptonshire]	possible hypobranchial
CAMSM J.67454	?	?	[Fletton, Northamptonshire]	caudal ray fragment with callus growth

CAMSM J.67455	?	? [Fletton, Northamptonshire]	striated caudal ray with flattened end
CAMSM J.67456	?	? [Fletton, Northamptonshire]	striated caudal ray with flattened end
CAMSM J.67457	?	? [Fletton, Northamptonshire]	striated caudal ray, possibly broken through callus
CAMSM J.67458	?	? [Fletton, Northamptonshire]	striated caudal ray, possibly broken through callus
CAMSM J.67459	?	? [Fletton, Northamptonshire]	caudal ray fragment
CAMSM J.67460	?	? [Fletton, Northamptonshire]	segment/callus in tail ray
CAMSM J.67461	?	? [Fletton, Northamptonshire]	stump of lepidotrichium (cast prior to growth ring sectioning by TJC)
CAMSM J.67462	?	? [Fletton, Northamptonshire]	segment/callus in tail ray
CAMSM J.67463	?	? [Fletton, Northamptonshire]	segment/callus in tail ray
CAMSM J.67464	?	? [Fletton, Northamptonshire]	possible hypobranchial
CAMSM J.67465	?	? [Fletton, Northamptonshire]	caudal ray fragment
CAMSM J.67466	?	? [Fletton, Northamptonshire]	segment/callus in tail ray, at bifurcation
CAMSM J.67467			gill raker
CAMSM J.67468			segment/callus in tail ray
CAMSM J.67469			segment/callus in tail ray, at bifurcation
CAMSM J.67470			striated caudal ray with flattened end
CAMSM J.67471	Henry Keeping ('H.K.')	1900 Fletton [Huntingdonshire]	hypobranchial (1)
CAMSM J.67472	Henry Keeping ('H.K.')	1900 Fletton [Huntingdonshire]	ceratobranchial fragment (1) connects to J.67479
CAMSM J.67473	Henry Keeping ('H.K.')	1900 Fletton [Huntingdonshire]	ceratobranchial fragment (1) connects to J.67477
CAMSM J.67474	Henry Keeping ('H.K.')	1900 Fletton	right cleithrum (1), ALMOST connects to J.67478

		[Huntingdonshire]	
CAMSM J.67475	Henry Keeping ('H.K.')	1900 Fletton [Huntingdonshire]	?left cleithrum (1)
CAMSM J.67476	Henry Keeping ('H.K.')	1900 Fletton [Huntingdonshire]	ceratobranchial fragment (1) connects to J.67480
CAMSM J.67477	Henry Keeping ('H.K.')	1900 Fletton [Huntingdonshire]	ceratobranchial fragment (1) connects to J.67473
CAMSM J.67478	Henry Keeping ('H.K.')		right cleithrum (1), ALMOST connects to J.67478
CAMSM J.67479	Henry Keeping ('H.K.')	1900 Fletton [Huntingdonshire]	ceratobranchial fragment (1) connects to J.67472
CAMSM J.67480	Henry Keeping ('H.K.')	1900 Fletton [Huntingdonshire]	ceratobranchial fragment (1) connects to J.67476
CAMSM J.67481		1897 Fletton [Huntingdonshire]	anal fin support
CAMSM J.67483	Henry Keeping ('H.K.')	1900 Fletton [Huntingdonshire]	pectoral fragment
CAMSM V.787			mid-line structure, see LEICT G.1105.1899
CAMSM X.39250			SWEEPINGS' TAIL SPECIMEN - probable caudal, the proximal part of X.50125, combined length of just over 1.3 metres
CAMSM X.50109	?	1898d Fletton [Huntingdonshire]	LP6 - left preopercular ridge (with articular points/callus growth?)
CAMSM X.50110	?	1898d Fletton [Huntingdonshire]	LP5 - dorsal fin spine (see LEICT G.474.1897 and G.475.1897) with anterior/posterior flexion
CAMSM X.50111	?	1898d Fletton [Huntingdonshire]	LP8 - dorsal fin spine
CAMSM X.50112	?	1898d Fletton [Huntingdonshire]	LP16 - right cleithrum
CAMSM X.50113	?	1899 Fletton [Huntingdonshire]	LP1 - right preopercular ridge
CAMSM X.50114	Henry Keeping ('H.K.')	1900 Fletton [Huntingdonshire]	LP4 - right ceratohyal
CAMSM X.50115	?	1901 Fletton [Huntingdonshire]	LP2 - hypobranchial
CAMSM X.50116	?	1901 Fletton	LP7 - (see 'yellow' identical bone in G.128.1900) - same

		[Huntingdonshire]	labels as J.27420-J.27423 (see also unnumbered Ox. Clay Fletton 1901 pyrite crisis with NO LP or other number)
CAMSM X.50117	?	1902 Whittlesea	LP9 - ?label like 46877 and 46878 - dorsal fin spine
CAMSM X.50118	?	? Whittlesea	LP3 - hypobranchial
CAMSM X.50119	?	? ?	LP10 - branchial arch fragment
CAMSM X.50120	?	? ?	LP11 - piece of ceratobranchial with mass of gill rakers (reminiscent of J.35320/LP.15)
CAMSM X.50121	?	? ?	LP12 - X.50121-X.50123 form two parallel ceratobranchials
CAMSM X.50122	?	? ?	LP13 - X.50121-X.50123 form two parallel ceratobranchials
CAMSM X.50123	?	? ?	LP14 - X.50121-X.50123 form two parallel ceratobranchials
CAMSM X.50124	?	? ?	LP15 - ceratobranchial fragment with mass of gill rakers - connects to J.35320
CAMSM X.50125	?	? ?	LP17 - distal part of probable caudal X.39250 (combined length of 1.3 metres)

Appendix IX Table 1b. Details of *Leedsichthys* specimens in New Walk and Leicester University Museum collections.

LEICT G1102.1899	Swales R Mr (gift)				Board of pectoral fin ray fragments
LEICT G1103.1899	Swales R Mr (gift)				Board of mounted gill rakers
LEICT G1104.1899	Swales R Mr (gift)				unident. bone - apparently connects to G.1105.1899 (see also two examples in P.6930 and one in V3363)
LEICT G1105.1899	Swales R Mr (gift)				unident. bone - apparently connects to G.1104.1899 (see also two examples in P.6930 and one in V3363)
LEICT G1106.1899	Swales R Mr (gift)				(from board, this could G1.2005 - else unseen)
LEICT G1107.1899	Swales R Mr (gift)				six bones: proximal end of L dentary, inferior end of L cleithrum, superior end of L cleithrum, end of ceratobranchial (like P.11823), plus two other bones only represented in V3363
LEICT G128.1900	Swales R Mr (gift)				left parietal, ?symplectic, basiocciput, left and right preopercular ridges, 4 ceratobranchials with pectoral fin raysand gill rakers showing fine structure, one piece like J.67421, one piece like LP.7/X.50116
LEICT G236.1902 /G520.1993	Swales R Mr (gift)			Oxford Clay of Peterborough	(B5, =G.520.1993) two fin ray/lepidotrichial elementsmost resemble pectoral rays, although slightly smoother than might be expected
LEICT G418.1956.15	Peterborough Museum Society (purchase) originally PJ Phillips		1919	Fletton	three bones: 1374= .5=left hypobranchial, .2=right hypobranchial, .4=end of ceratobranchial (.1 and .3 unseen)
LEICT G471.1897	Swales R Mr (gift)/Pocock	15/7/1896		Oxford Clay of Peterborough	dorsal fin spine - resembles a proximal radial (although groove poorly defined on one side)
LEICT G472.1897	Swales R Mr (gift)/Pocock	15/7/1896		Oxford Clay of Peterborough	dorsal fin spine
LEICT G473.1897	Swales R Mr (gift)/Pocock	15/7/1896		Oxford Clay of Peterborough	dorsal fin spine
LEICT G474.1897	Swales R Mr (gift)			Oxford Clay of Peterborough	(B6) dorsal fin spine, with anterior/posterior flexion
LEICT G475.1897	Swales R Mr (gift)			Oxford Clay of Peterborough	(B6) dorsal fin spine

LEICT G476.1897	Swales R Mr (gift)		Oxford Clay of Peterborough	unseen
LEICT G477.1897	Swales R Mr (gift)		Oxford Clay of Peterborough	unseen
LEICT G478.1897	Swales R Mr (gift)		Oxford Clay of Peterborough	unseen
LEICT G479.1897	Swales R Mr (gift)		Oxford Clay of Peterborough	unseen
LEICT G765.1898	Swales R Mr (gift)			R hyomandibula
LEICT G343.1896	Swales R Mr (gift)		Oxford Clay of Peterborough	(B2) dorsal fin spine, 'clavicular' form
LEICT G344.1896	Swales R Mr (gift)		Oxford Clay of Peterborough	(B2) dorsal fin spine, see V3363 for one
LEICT G345.1896	Swales R Mr (gift)		Oxford Clay of Peterborough	(B2) dorsal fin spine
LEICT G451.1992	Swales R Mr (gift)			.1-.7=(former 02/107 or 107Xw'02) - unseen, but probably pectoral fin-rays
LEICT G519.1993	Swales R Mr (gift)	1902	Oxford Clay of Peterborough	.1-.7=dorsal fin spines (former 02/235 or 235Xw'02 "ichthyosaur ribs") - unseen
LEICT G1312.1899	purchase unknown		Oxford Clay of Peterborough	(B1) four proximal radials and two dorsal fin spines (including one possible anterior/posterior flexion).
LEICT G393.1896	Swales R Mr (gift)		Oxford Clay of Peterborough	unseen
LEICT G3348.1898	purchase unknown		Oxford Clay of Peterborough	unseen
LEICT G1.2005				parasphenoid (could be G.1106.1899)
LEIUG 96085	David Michael Martill	1987	Dogsthorpe Pit	gill raker
LEIUG 96086	David Michael Martill	1979	[Market Deeping]	fragments of actinotrichia, gill-rakers, fin-rays, ceratobranchials
LEIUG 96087	P.C. Schultz	1973	[Orton Pit]	ceratobranchial, pectoral fin-ray and gill raker fragments - /24 has special gill raker feature
LEIUG 114604	Martill & Hollingworth	1991	LBC pit, Calvert	concretion with pectoral fin-rays and two radiales, also associated pectoral fin-ray, preopercular and cleithral fragments

Appendix IX Table 1c. Details of *Leedsichthys* specimens in Oxford University and Peterborough Museum collections.

OUMNH J.1803	ET Leeds, Woodstock Road			dorsal fin spine - was on wall of his house until 1950 - as collected by his dad.
OUMNH J.1803/1	A.M. Bell, Balliol College	1894	OC of Wolvercote, NW of Oxford	Lived in north Oxfordshire and donated occasional pieces.dorsal fin spine
PETMG F1				hyomandibula, dorsal fin spine, hypobranchial - other unaudited material at PETMG
PETMG F2	John Phillips			1425 - hypobranchial - other unaudited material at PETMG
PETMG F34	John Phillips		King's Dyke	1466 - partial skull with damaged remains of skull roof, branchial basket and jaws
PETMG F121	David Michael Martill	1984	Buntings Lane, near Farcet	lepidotrichial fragments, including pectoral fin rays
PETMG F124				with F.121 - lepidotrichial fragments
PETMG F174	Liston/Dawn/Martill et al.	2001-2003	Star Pit, Whittlesey	ARISTON - UNDER PREP. - paired pectoral fins (/10025, /10002), preopercles and hyomandibulae; fused parietals and paired dermopterotics; /2052 gill raker figured, /10004 right cleithrum, /182 left preopercle, /245 radiale I, /263 radiale II, /264 lpdt, dorsal fin spines, hypobranchial, ceratobranchial III, actinotrichia, ceratohyal, many gill rakers
PETMG R189				dorsal fin spine, hypobranchial - extracted from Muraenosaurus leedsi specimen.

Appendix IX Table 1d. Details of *Leedsichthys* specimens in Natural History Museum (London) collections.

Specimen number	Number of parts	Description (as given in BMNH accession and purchase registers)	Description
BMNH P.6921	1,133	"Associated series of bones, the type specimen..."***//"Bones of Leedsia 180 specimens" [part of batch]	gill rakers (89), ceratobranchials (2 x first), epibranchials (2 x second plus 1 indet.), lepidotrichia, parietals, left cleithrum, cleithrum-like element, hypobranchials (4, 2 red), hypobranchial-like mass, distal actinotrichia (4), radiale II, radiale I, thin unknown, left ceratohyal, partial right ceratohyal, ?branched supraneural, ?bromalite/coprolite, associated Pachymylus tooth plate, 17 lengths of dfs (of which 10 red-marked), 1c-b + pec (mainly unprepared from the clay) + caudal fin-rays, 2 bones with callus breaks
BMNH P.6922	8	""Preoperculum or clavicle", doubtfully associated with above, described ibid. p.453, no.6."//[as P.6921]	right preopercle with 2 fragments
BMNH P.6923	27	"A pair of large flat bones, and two supposed "branchial arches". (4)"//[as P.6921]	2 ceratobranchials with 2 unidentified cranial elements
BMNH P.6924	19	"Series of supposed "branchiostegal rays", found associated. (10)"[as P.6921]	dorsal fin spines (7)
BMNH P.6925	243	"Miscellaneous "branchiostegal rays", one noticed loc. cit. p.453 (25)"[as P.6921]	dorsal fin spines (30 plus frags- includes robust curved element from type description - possibly some from P6924, noting callus), proximal radials (11 plus frags), caudal fin ray fragments (11), left preopercular ramus, cleithral fragments, ?ceratohyal fragment, left ?maxillary fragment
BMNH P.6926	199	"Two associated portions of supposed branchial arches. (2)"[as P.6921]	2 ceratobranchials with pectoral fin ray fragments
BMNH P.6927	37	"Two associated undetermined bones. (2)"[as P.6921]	cleithrum-like fragment, right ?preopercle-like bone (compare with Fig. 8.35 top) 575mm long plus 2 other preopercle-like fragments (probably from other specimens)
BMNH P.6928	35	"Associated series of bones. (12)"[as P.6921]	proximal radial fragment, ceratobranchial, left ceratohyal, right anal fin support, dorsal fin spine fragment, 9 'tips' plus V787-like bone
BMNH P.6929	83	"Associated fin-rays."//[as P.6921]	pectoral fin ray fragments
BMNH P.6930	352	"Miscellaneous bones."//[as P.6921]	epibranchial (1), left supramaxilla, both nasals, caudal fin rays, paired cleithrum-like frags-undeveloped???, ceratohyal (left), ceratobranchials (3), possible paired entopterygoids?, ridged dermatocranial element (postparietal?), roughened dermatocranial elements, possible dermopterotic, fragments of parasphenoid, ?small parietal?

BMNH P.8609		5	" - (1)"//"unnamed fish plates and bones"	right cleithrum with ?ceratobranchial fragment and two lepidotrichial fragments (one with ?callus)
BMNH P.8610		17	"gill-rakers. (12)"//"unnamed fish plates and bones"	gill rakers (17)
BMNH P.10000	NOL+358+93+393+58		"Tail + associated bones (1)"//"A set of fish remains of Leedsia problematica"	both caudal lobes, ?left pectoral fin fragment, pyritised ceratohyal, left hyomandibula, both cleithra, both epibranchial Is, 3 ceratobranchial fragments, parasphenoid, 2 'preopercle-esque' bones, gill rakers (possibly one with 'mesh'), lepidotrichial fragments, 3 ?pliosaur epipodials are associated with this specimen
BMNH P.10156	NOL+...		"Hyom. + br. arches. (1)"//"Leedsia problematica, hyomandibular + branchial arches"	gill basket, left hyomandibula, ?pectoral fin rays, left preopercular ridge (with ?epibranchial fragment), both hypohyals, a left hypobranchial I, both hypobranchial IIs, both ceratobranchial Is, both ceratobranchial IIs, both ceratobranchial IIIs, both ceratobranchial IVs, basibranchial IV, fused ceratobranchial arch V, ?angular/?supraangular,
BMNH P.11823		405	"Hyomandibulars, branchials etc. (1)"//"Various bones of Leedsia, etc."	Pair of hyomandibulae, ?left ?parietal, ceratohyal, ?left ?subopercle, bone with large ?nerve canal, 3 hypobranchials, 6 ceratobranchials, 3 epibranchials (2 x I and 1 x II), boss-shaped bone, lepidotrichial fragments (probably non-pectoral)
BMNH P.11824		34	"Gular, epihyal, branchials, etc.(1)"//"Various bones of Leedsia, etc."	right parietal plus unidentified dermatocranial element (treated) PLUS London material....
BMNH P.11825		20	"Vertebral arches (1)"//"Various bones of Leedsia, etc."	Robust curved element (used as relative mass indicator '34') plus 12 ?dfs fragments including 5 fairly complete representatives
BMNH P.11826		7	"Fused ditto. (1)"//"Various bones of Leedsia, etc."	3-way branching ?dorsal fin spine or ?fused supraneural
BMNH P.12534		16	"(3 bones)"//part of 15 fish-remains	left dermosphenotic,odd branched bone plus unidentified dermatocranial element
BMNH P.47412		61	Liverpool specimen - "dissociated bones"	ceratohyal plus lepidotrichial fragment
BMNH P.66340	Alfred Nicholson Leeds (via Liverpool University/Museum)		Leeds '11'	left hypohyal, right dentary, ?angular/?supraangular, with unidentified element vaguely similar to ceratohyal
BMNH P.66341	Alfred Nicholson Leeds (via Liverpool University/Museum)			dorsal fin spines (6, including 2 robust curved elements)
BMNH P.66342	Alfred Nicholson Leeds (via Liverpool University/Museum)			dorsal fin spines (10 - 5 complete)

Appendix IX Table 1e. Details of *Leedsichthys* specimens collected by Alfred Leeds in other museum collections.

GLAHM V3362		1	branching caudal fin ray (1225mm long)
GLAHM V3363		904	12 numbered and paired from January 1915 sale, left maxilla, left ceratohyal, left ?preopercle, left preopercular ridge, 'ribs', anal fin supports (5), proximal radials (8), right parietal, 5 hypobranchials, 4 ceratobranchials (parts 6 & 7), ?4 epibranchials (parts 9 & 10), dorsal fin spines (63), 2-way branching fused supraneural, robust curved elements (6), cleithral fragment (part 8 - former 'dentary'), 2 ?hyomandibulae (parts 1 & 5), caudal fin ray fragments, 2 gill-rakers, callus broken bone, unidentified dermatocranial elements (paired 12 & 4), 11 unidentified bone, butterfly' bone (pathological cleithum?), basiocciput
NMGW 19.96.G8		68 Leeds no.25	2 hypobranchials, 3 ceratobranchials, left preopercular ridge, pectoral fin rays
NMGW 19.96.G9		12	robust curved element ('20'), dorsal fin spines (8, only 1 incomplete)

Appendix IX Table 1f. Details of miscellaneous other *Leedsichthys* specimens.

BMNH 32581		1 "Branchiostegous rays of fish Oxford Clay - "Dives - Vaches Noire"" from M'sieu Tesson of Caen in 1857.	Concretion of disarticulated gill rakers
BMNH 46355		1 Christian Malford specimen - bought from William Cunningham Esq. in February 1875 - originally figured as reptile ribs?	Isolated fin ray fragment
BMNH P.62054	I. Crowson	1985 Buntings Lane	?pectoral fin rays
	1 Nick Oliver	1998 Kempston Quarry	3D preserved ceratobranchials on underside of dermatocranium
	2 Nick Oliver		
	Alan Dawn	Quest Pit, Stewartby	fimbriated tip of dorsal fin spine

Chapter 2: Figures

Figure 2.1. The associated group of gill rakers of *Leedsichthys* referred to by Woodward in his original description (Smith Woodward 1889b). From the Oxford Clay of Vaches Noire, Normandy, France. BMNH 32581. Scale bar = 50mm.

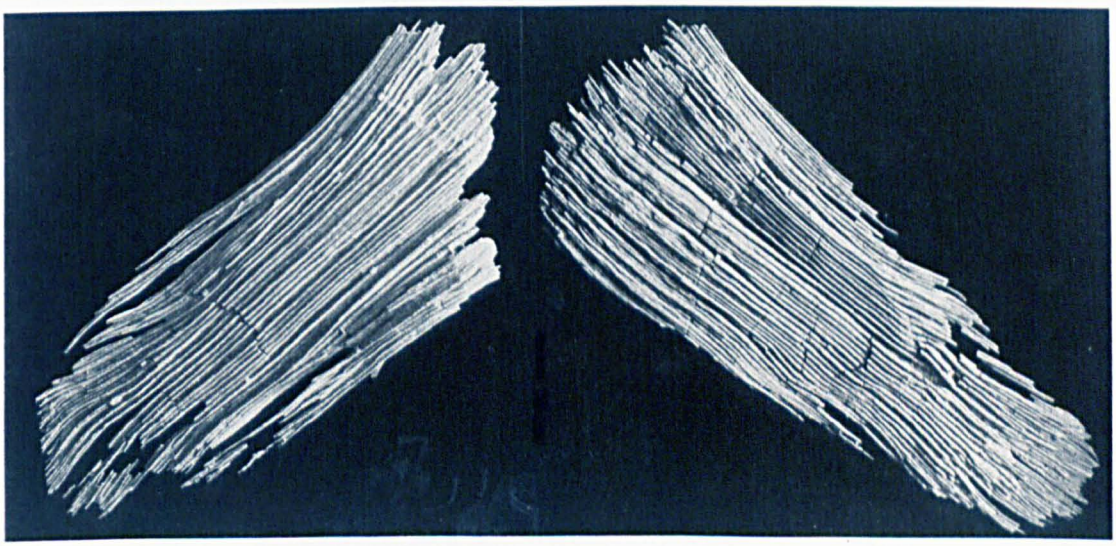


Figure 2.2. The tail specimen BMNH P 10000 found by Alfred Leeds in March 1898. It is unclear which is the superior, and which the inferior, lobe. For scale refer to fig. 3.1. Photograph by R. Branson, 1985, reproduced by courtesy of D. M. Martill.

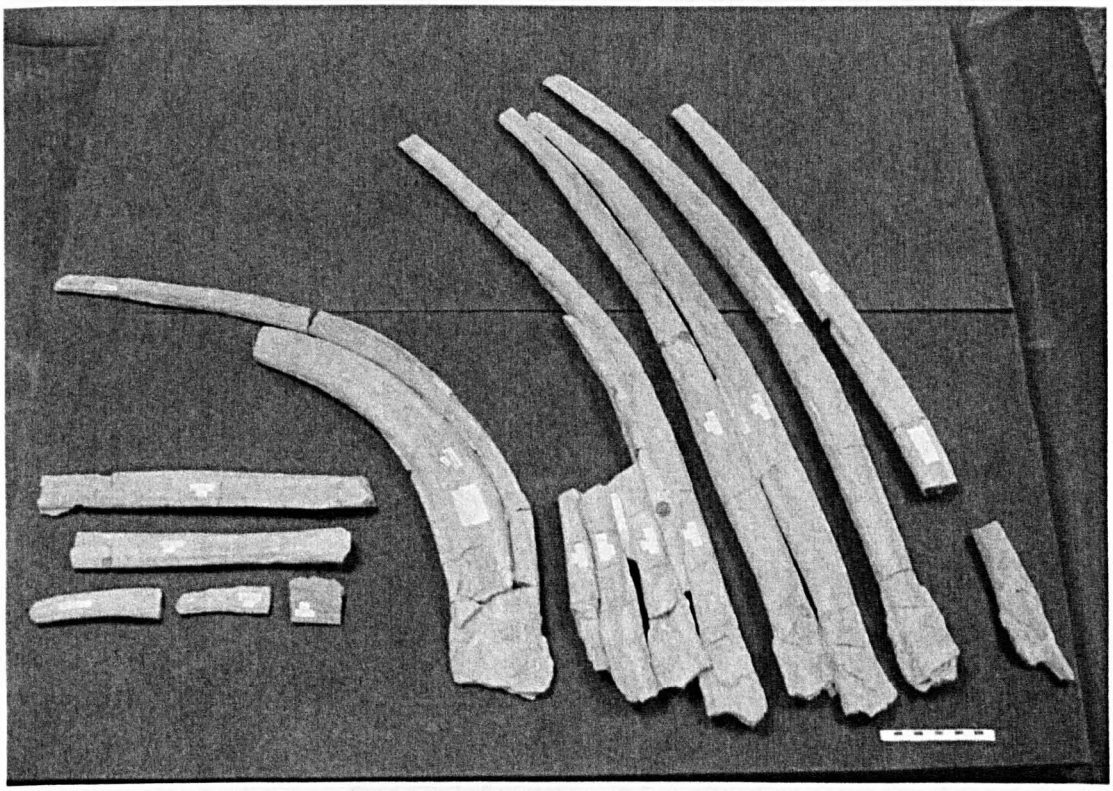


Figure 2.3. The bones of *Leedsichthys*, misidentified and figured as stegosaur tail spines by Von Huene in 1901. CAMSM J46873. Scale bar (in bottom right of picture) = 100mm.

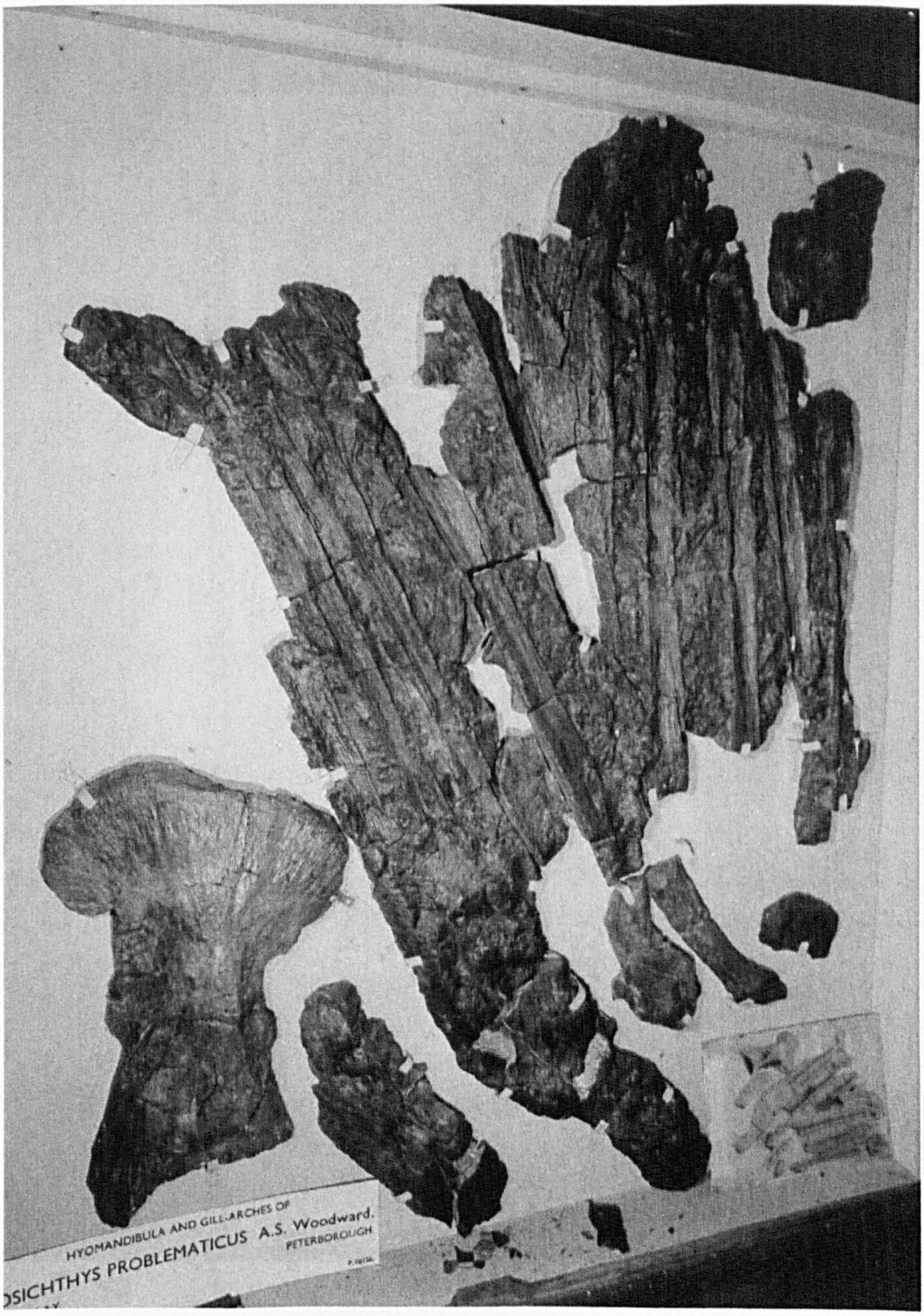


Figure 2.4. The gill basket specimen BMNH P 10156, over 2 metres high, on display in The Natural History Museum, London, c. 1985. © The Natural History Museum, London.

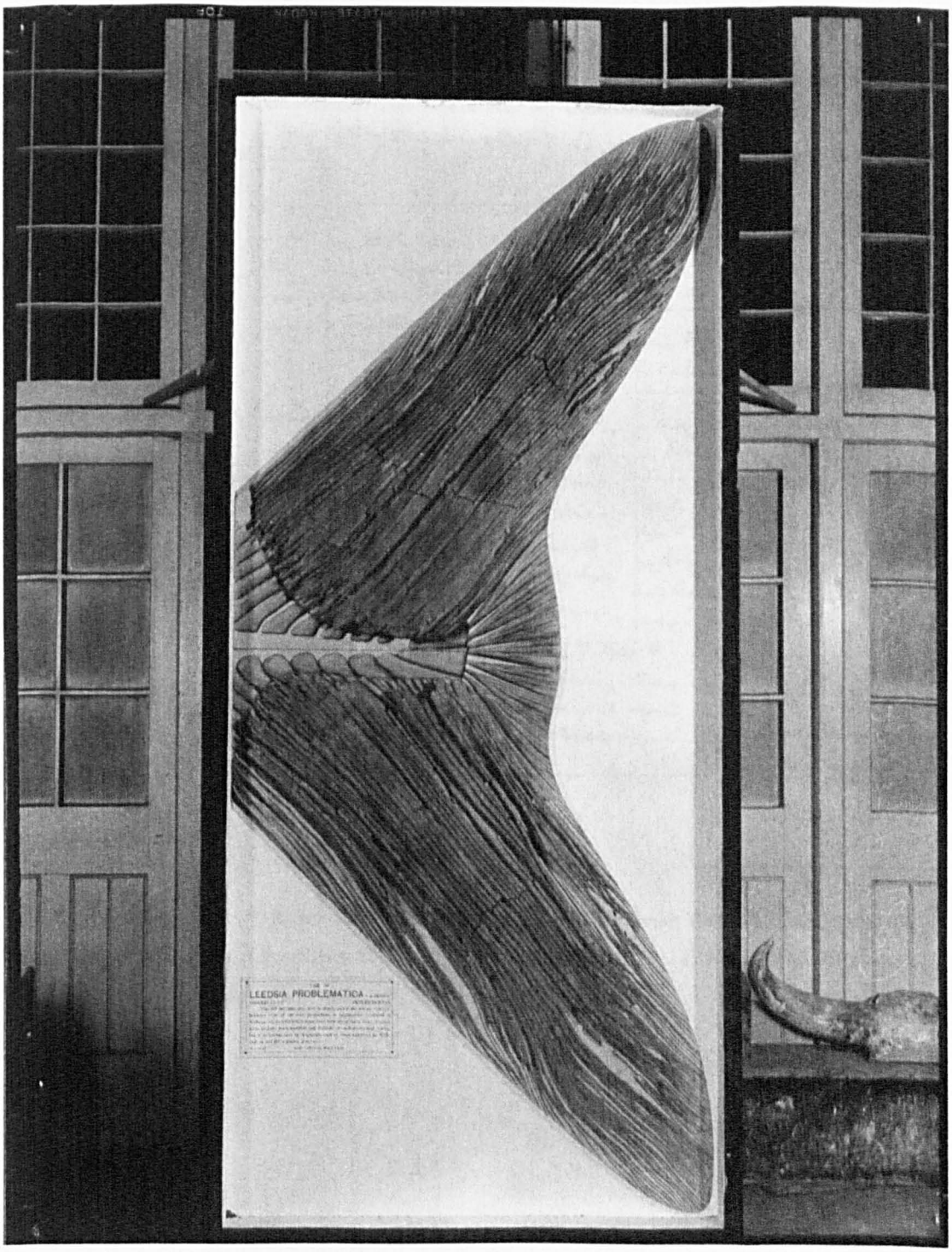


Figure 2.5. The tail specimen BMNH P 10000 on display in The Natural History Museum, London, in September 1937. Peripheral skeletal components not recovered from the site have been added as a painted backdrop. For scale refer to fig. 3.1. © The Natural History Museum, London.

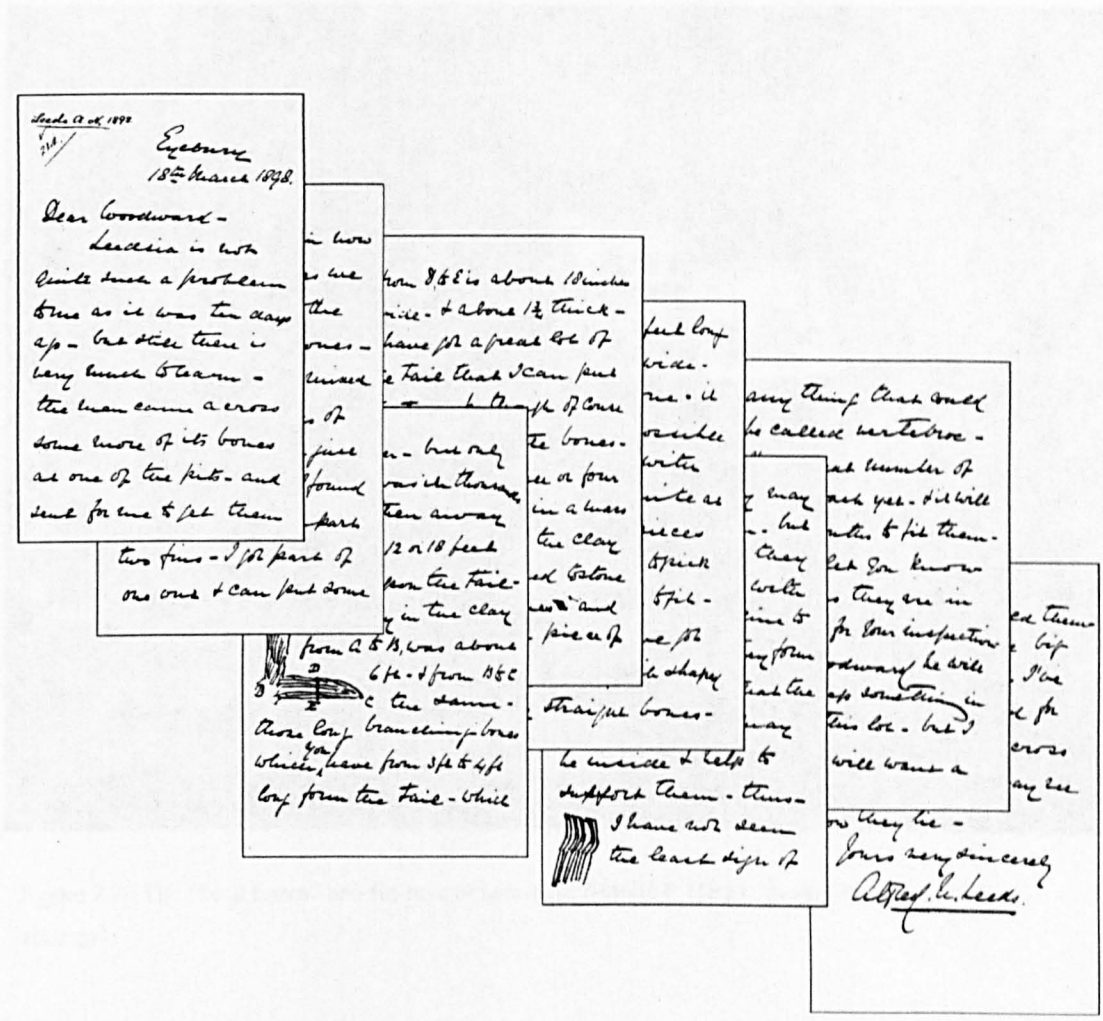


Figure 2.6. The letter of 18th March 1898 from Alfred Leeds to Arthur Smith Woodward, discussing the disposition of a specimen that includes the BMNH P 10000 tail, design by L. F. Noè, © The Natural History Museum, London.

Figure 2.7. The "head bones" and fin-rays of specimen BMNH P.11823. Scale bar, bottom right = 100mm.

Figure 2.8. The 904 parts of GLAHM V3363, spread out in the Research Store of the Hunterian Museum, University of Glasgow, to reveal the extent of the Glasgow specimen of *Leedsichthys problematicus*. Dr. J. W. Faithfull (1.8 metres high) is included for scale.

Chapter 3: Figures

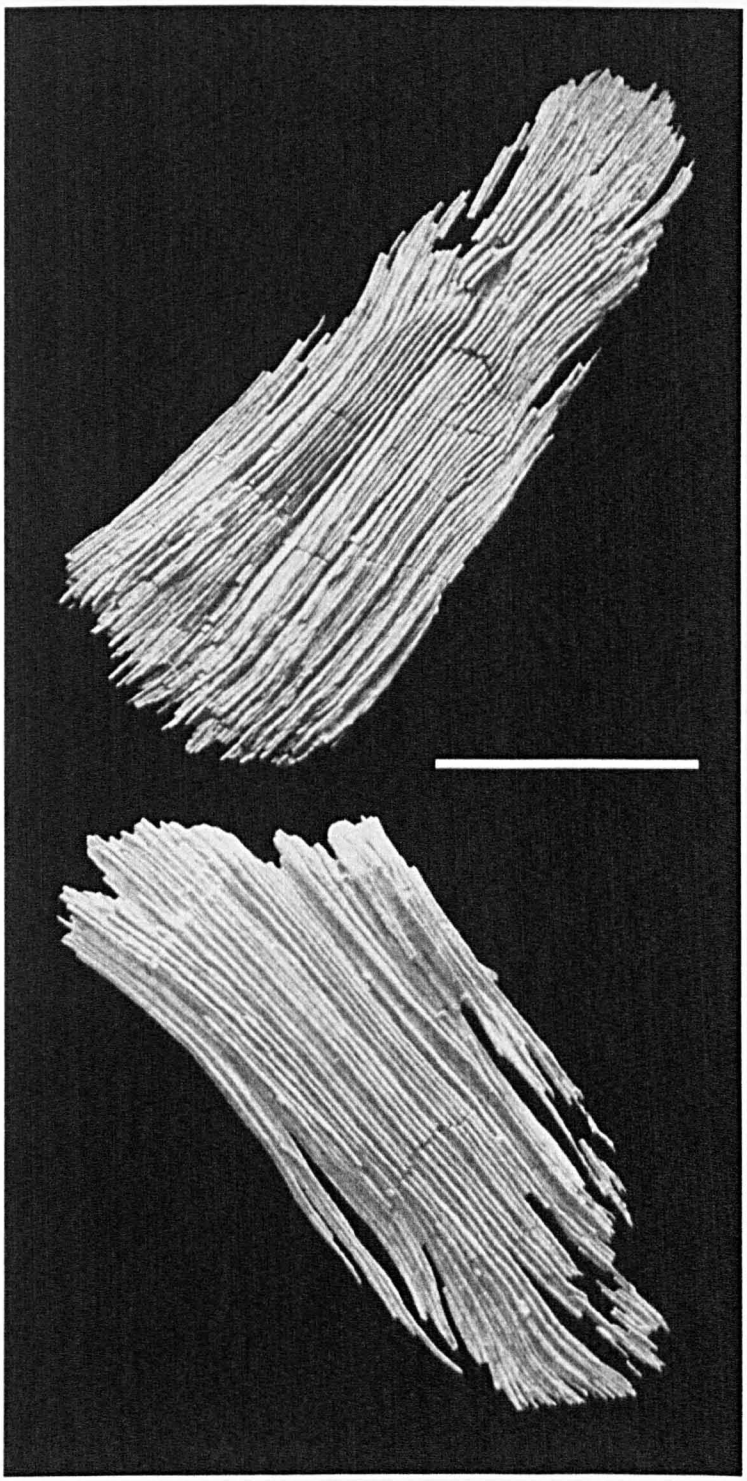


Figure 3.1. The bones of the tail of *Leedsichthys problematicus* Woodward 1889[a] P.10000. The orientation of the lobes (dorsal or ventral), and the angle at which they met is unknown. Scale bar = 0.5 m. Previously figured by Martill (1988, Figure 1) and Martill and Hudson (1991, Plate 43). Photograph by Rod Branson, reproduced courtesy of David Martill.

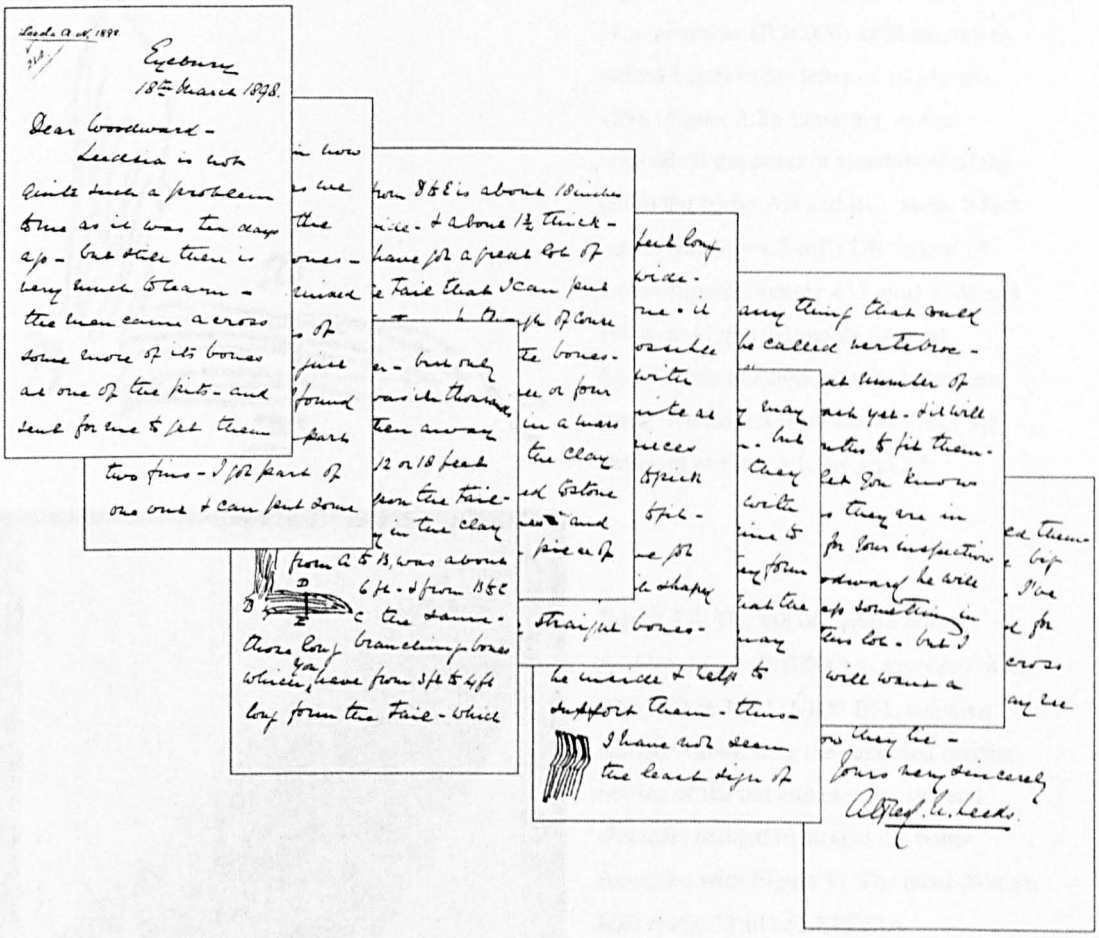


Figure 3.2. An eight-page letter from Alfred Nicholson Leeds to Arthur Smith Woodward dated 18 March 1898 (The Natural History Museum Official Archives, NHM-GL DF100/31) giving details of the excavation of P.10000, the tail and associated specimens of *Leedsichthys problematicus* Woodward 1889[a]. The illustrations appear as Figure 3.3 (the tail) and Figure 3.6 (the proposed dorsal fin support); for a transcript of the letter is included within the text of this article. Reproduced by permission of the Trustees of The Natural History Museum.

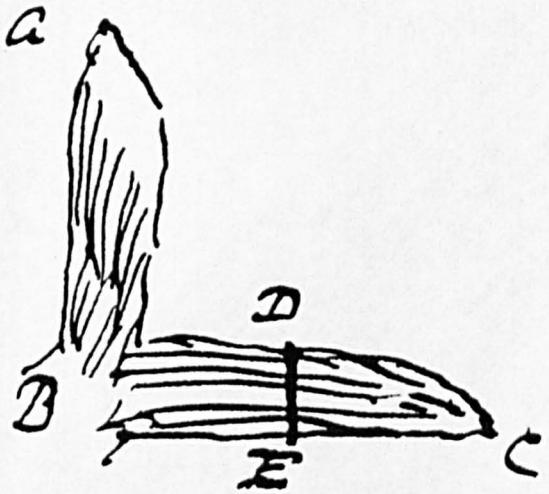


Figure 3.3. The tail of *Leedsichthys problematicus* (P.10000) as illustrated by Alfred Leeds in his letter of 18 March 1898 (Figure 3.2). Lettering, as the original: B the point of attachment of the tail to the body; AB and BC "about 6 feet [approximately 1.8 m]"; DE "about 18 inches [approximately 457 mm] wide and 1¾ inches [approximately 44 mm] thick". Note the angle at which they are illustrated differs from the way they are mounted in Figs. 3.1, 3.4 and 3.5.

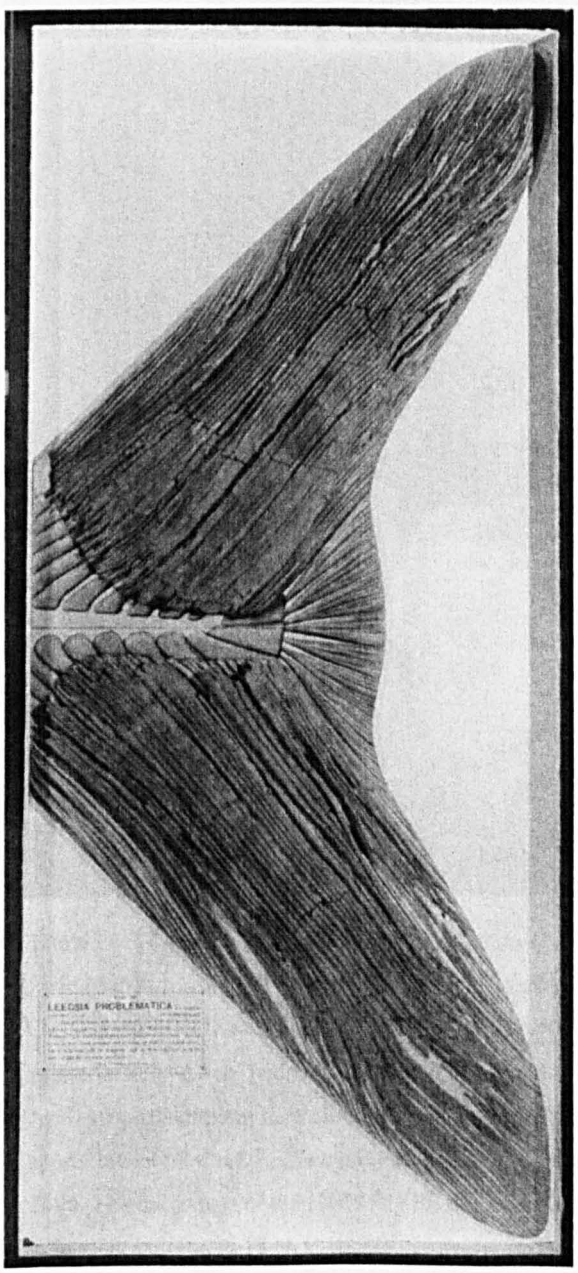


Figure 3.4. The tail of *Leedsichthys problematicus* (P.10000) as mounted in the BM(NH) in 1937 (NHM ESL negative number 1660); note the supposed original outline of the tail and missing skeletal elements painted in around the bones (compare with Figure 1). The label (bottom left) reads: "Tail of LEEDSIA PROBLEMATICA A.S.WOODW[ARD]. OXFORD CLAY. PETERBOROUGH. This tail measures nine feet [approximately 2.7 m] in depth, and if the fish to which it belonged were the same proportions as *Hypsocormus* exhibited in Wall-case 13, its total length must have been about thirty feet [approximately 9.1 m]. *Leedsia* seems to have been toothless and destitute of ossified vertebral centra, but it is known only by fragments such as those exhibited in Wall-case 14 and the adjoining panel ←. [P.10000] (Leeds Collection, March 1899)." Note the use of the outdated binomial 'Leedsia problematica'. Reproduced by permission of the Trustees of The Natural History Museum.

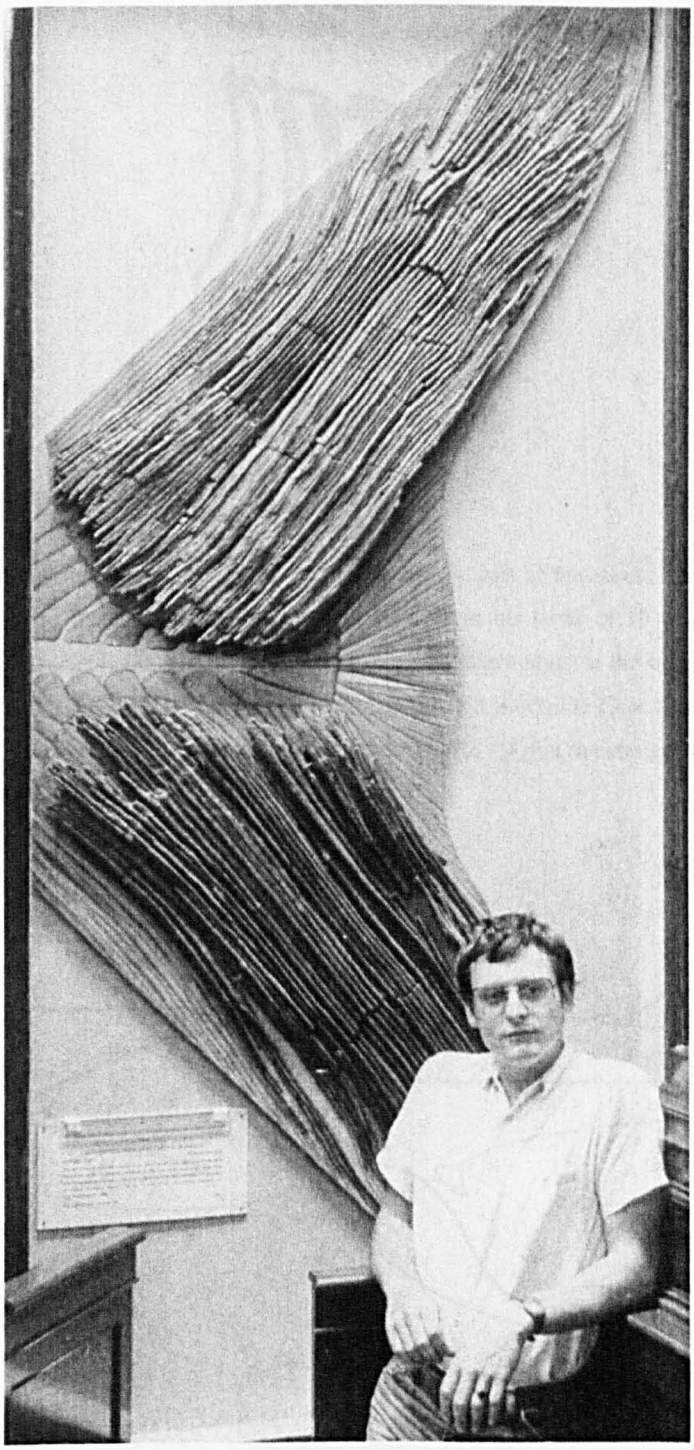


Figure 3.5. The tail of *Leedsichthys problematicus* (P.10000) as displayed in the BM(NH) in 1985, with David Martill for scale. The label (bottom left) reads: "Tail of LEEDSICHTHYS PROBLEMATICUS A.S. Woodward. OXFORD CLAY. PETERBOROUGH. This tail measures about nine feet [approximately 2.7 m] in depth. If the fish to which it belonged were of the same proportions as the *Hypsocormus* exhibited in Wall-case IV, its total length must have been about twenty-five feet [approximately 7.6 m]. *Leedsichthys* seems to have been toothless and destitute of ossified vertebral centra. The tail is part of the HOLOTYPE described by A.S. Woodward in 1889. A.N. Leeds Collection, purchased 1899. P.10000". Note the updated binomial and the incorrect emendation (by comparison to Figure 3.4) stating that the tail is part of the holotype. Photograph by Rod Branson, reproduced courtesy of David Martill; a copy of this photograph has been lodged with the NHM.

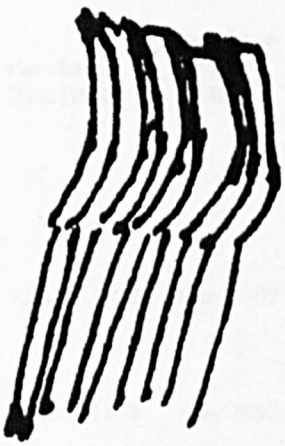


Figure 3.6. A hypothetical reconstruction of part of the absent dorsal fin of *Leedsichthys problematicus* (P.10000), as illustrated by Alfred Leeds in his letter of 18 March 1898 (Figure 3.2). Alfred Leeds describes the illustration: "At present I have got none of the big rib shaped + long straight bones - but live hoping they may come across them - but it is quite clear they have nothing to do with the head - I incline to the idea that they form the back fin - + that the straight bones may be inside + help to support them - thus".

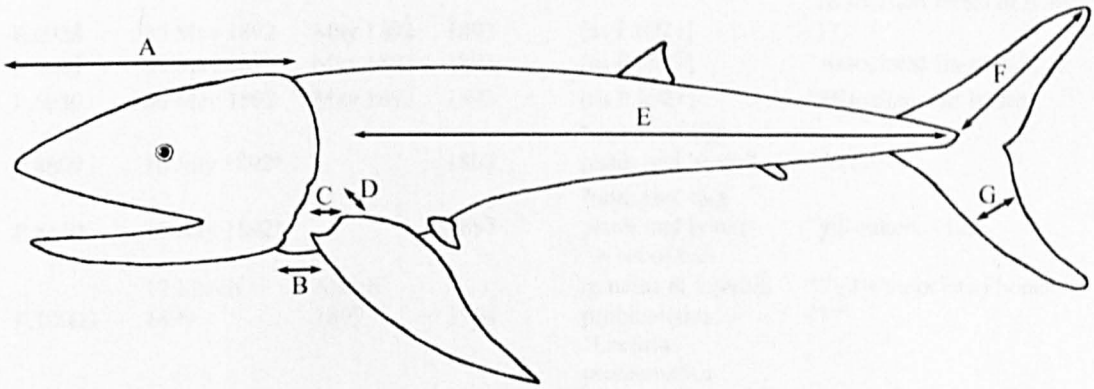


Figure 3.7. A hypothetical reconstruction of *Leedsichthys problematicus* P.10000 based on the information given by Alfred Leeds in his letter of 18 March 1898 (Figure 3.2) and estimates of other dimensions not given therein. The size of the head (A) is unknown (conservatively estimated at 1.0 m), but just beyond (B; ?0.5 m) lay two fins, here interpreted as the paired pectorals (C, the anteroposterior length of the fins proximally; ?0.5 m), a good distance apart (D, the width of the body), with the tail up to 5.5 m beyond the fins (E). The tail measured 1.5 m along each lobe (F) and was just less than 0.5m across the middle of one lobe and nearly 45 mm thick (G). If the anteroposterior length of the tail was originally 1.5 m, then the fish may be estimated at about 9.0 m in total length. Outline image (modified from Martill, 1986 original reconstruction by Paul Policott).

Chapter 3: Tables

Specimen number	Purchase Date (P.R.)	Purchase Date (A.R.)	Accession Date (A.R.)	Description (P.R.)	Description (A.R.)
P.6921	30 May 1892	May 1892	1893	"Bones of Leedsia 180 specimens" [part of batch]	"Associated series of bones, the type specimen described in Geol. Mag. [3] vol. vi. 1889, pp. 451-454, & gill-rakers descrd. & figd. Ibid. vol. vii. P.292, pl.x f. 9,10 (70, about)"
P.6922	30 May 1892	May 1892	1893	[as P.6921]	""Preoperculum or clavicle", doubtfully associated with above, described ibid. p.453, no.6."
P.6923	30 May 1892	May 1892	1893	[as P.6921]	"A pair of large flat bones, and two supposed "branchial arches". (4)"
P.6924	30 May 1892	May 1892	1893	[as P.6921]	"Series of supposed "branchiostegal rays", found associated. (10)"
P.6925	30 May 1892	May 1892	1893	[as P.6921]	"Miscellaneous "branchiostegal rays", one noticed loc. cit. p.453 (25)"
P.6926	30 May 1892	May 1892	1893	[as P.6921]	"Two associated portions of supposed branchial arches. (2)"
P.6927	30 May 1892	May 1892	1893	[as P.6921]	"Two associated undetermined bones. (2)"
P.6928	30 May 1892	May 1892	1893	[as P.6921]	"Associated series of bones. (12)"
P.6929	30 May 1892	May 1892	1893	[as P.6921]	"Associated fin-rays."
P.6930	30 May 1892	May 1892	1893	[as P.6921]	"Miscellaneous bones."
P.8609	16 July 1892*		1897	"unnamed fish plates and bones"	" - (1)"
P.8610	16 July 1892*		1897	"unnamed fish plates and bones"	"gill-rakers. (12)"
P.10000	17 March 1899	March 1899	1904	"A set of fish remains of Leedsia problematica"	"Tail + associated bones (1)"
P.10156	22nd July 1905	[July 1905	1905	"Leedsia problematica, hyomandibular + branchial arches"	"Hyom. + br. arches. (1)"
P.11823	28 July 1898	July 1898	1915	"Various bones of Leedsia, etc."	"Hyomandibulars, branchials etc. (1)"
P.11824	28 July 1898	July 1898	1915	"Various bones of Leedsia, etc."	"Gular, epihyal, branchials, etc.(1)"
P.11825	28 July 1898	July 1898	1915	"Various bones of Leedsia, etc."	"Vertebral arches (1)"
P.11826	28 July 1898	July 1898	1915	"Various bones of Leedsia, etc."	"Fused ditto. (1)"
P.12534	28 June 1920**	[June 1920	1920	part of 15 fish-remains	"(3 bones)"

*Purchase via Chas Davies Sherborn FGS for Alfred N. Leeds.
**Purchase from Mrs Leeds, after the death of her husband.

Table 3.1. *Leedsichthys* specimens bought by the BMNH from the Leeds family

Chapter 4: Figures

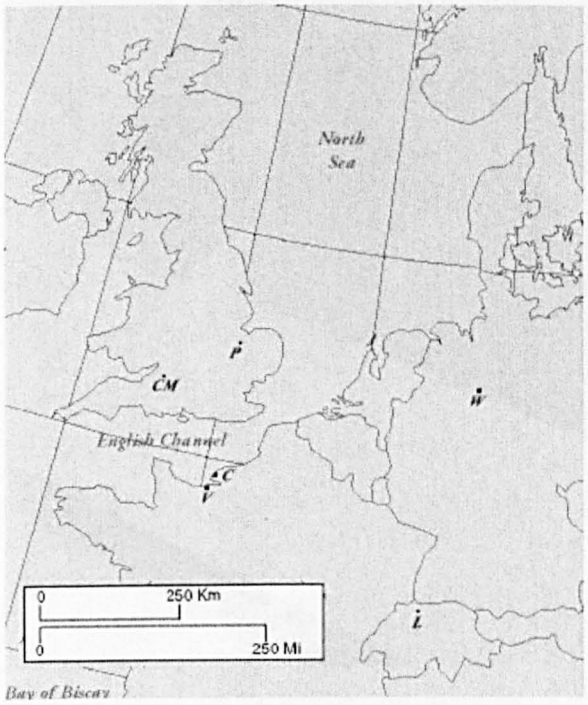


Figure 4.1. Map showing European localities where *Leedsichthys* remains have been uncovered. C = Cap de la Hève; CM = Christian Malford; L = Liesberg P = Peterborough; V = Villers-sur-mer; W = Wiehengebirge.

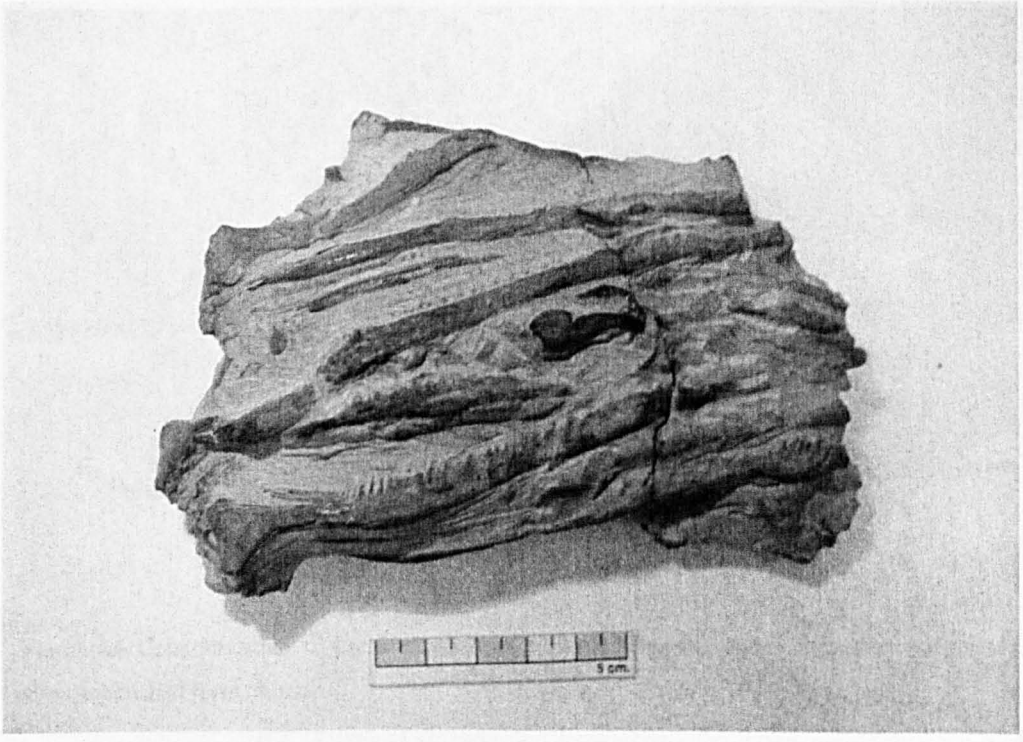


Figure 4.2. BMNH 32581, a concretion of disarticulated gill rakers from Vaches Noire, the earliest-collected specimen of *Leedsichthys*. Scale bar = 50mm.

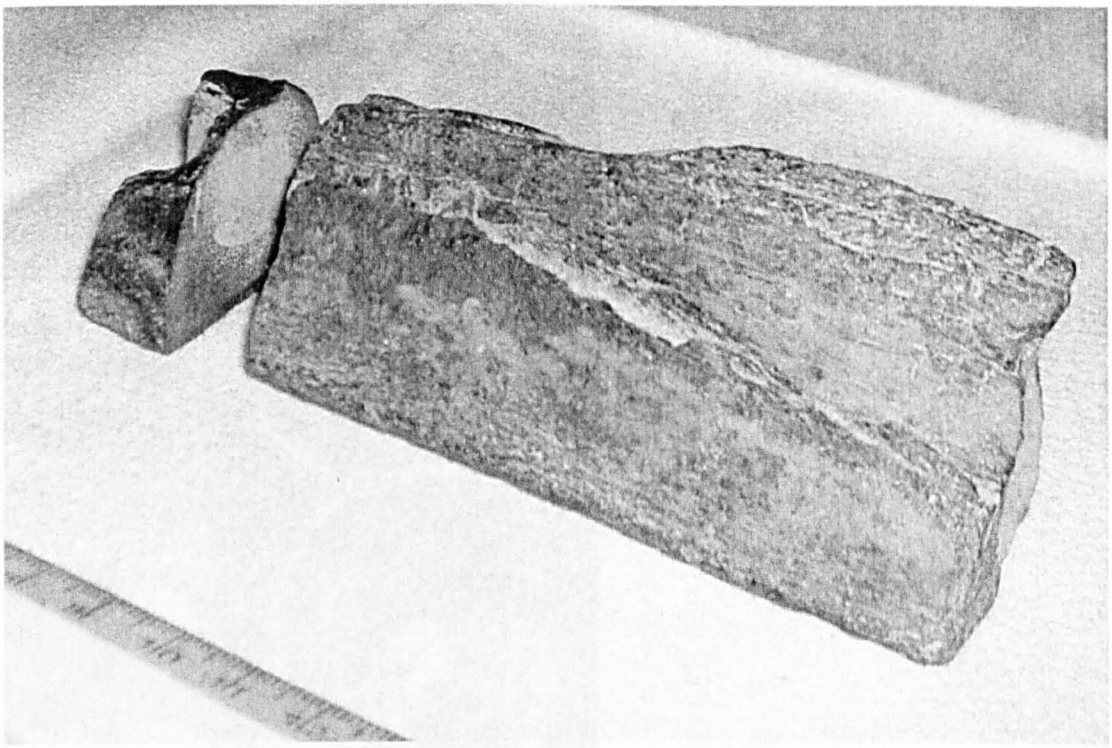


Figure 4.3. Ceratobranchial of *Leedsichthys* from the collection of G. and E. Pennettier, in dorsolateral view to show uncrushed form of bone. Scale bar marked in centimetres.

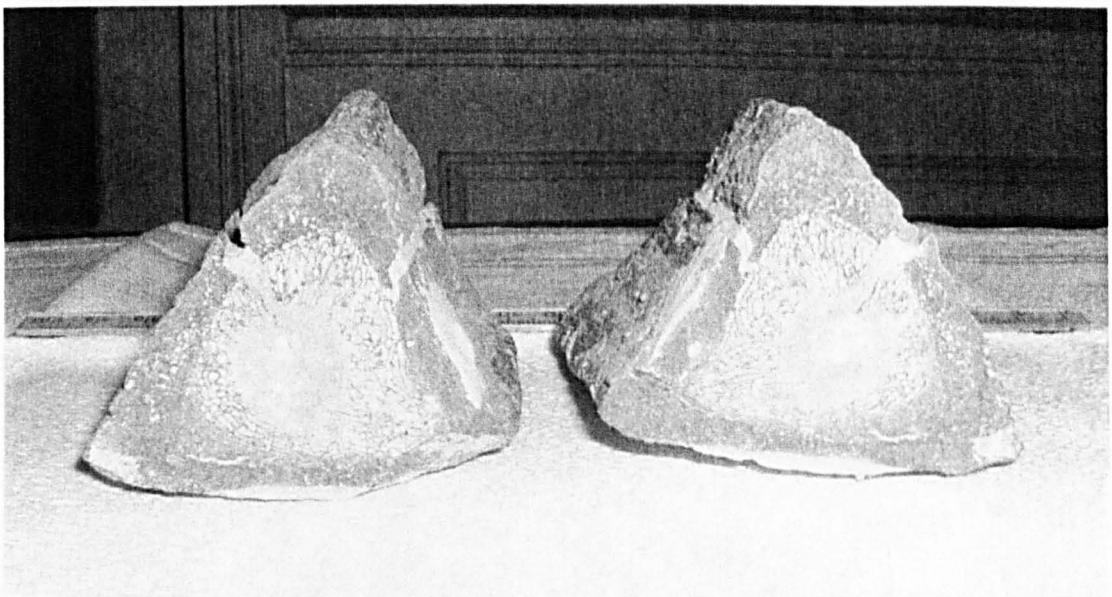


Figure 4.4. Ceratobranchial of *Leedsichthys* from the collection of G. and E. Pennettier, sectioned to show uncrushed form of bone.

Figure 4.5. Transverse section of ceratobranchial under microscope from the collection of G. and E. Pennettier, showing extensively remodelled lamellar bone. Image courtesy of N. Bardet.

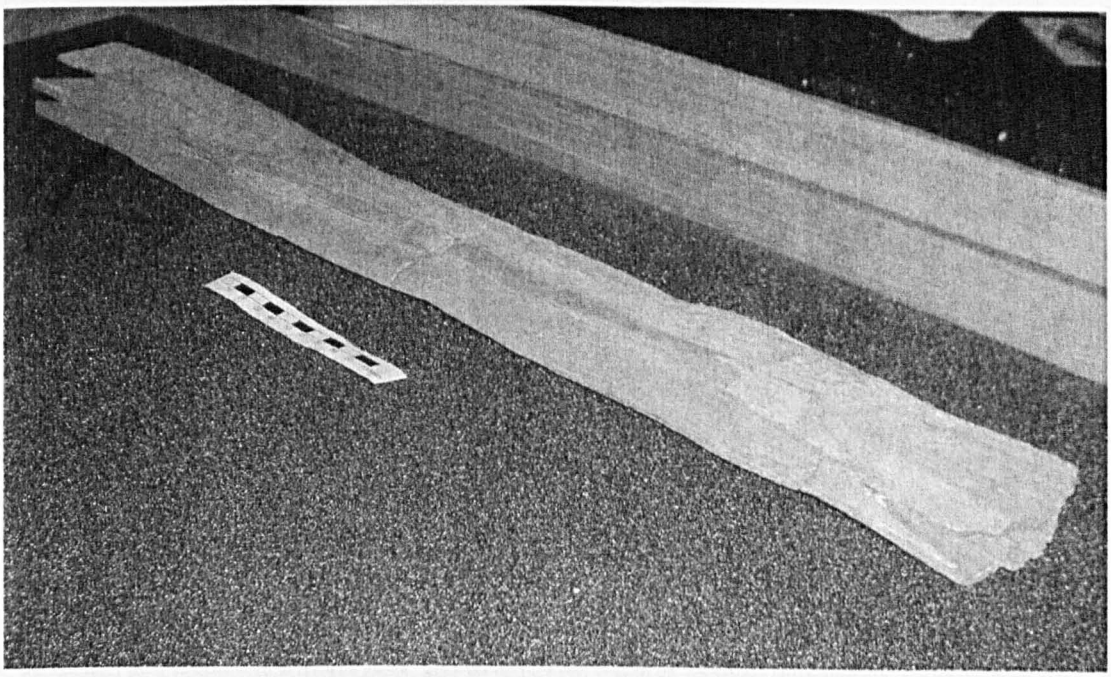


Figure 4.6. Ceratobranchial of *Leedsichthys*, part of the holotype specimen BMNH P.6921, in dorsolateral view, to show flattening of bone. Scale bar = 100mm.

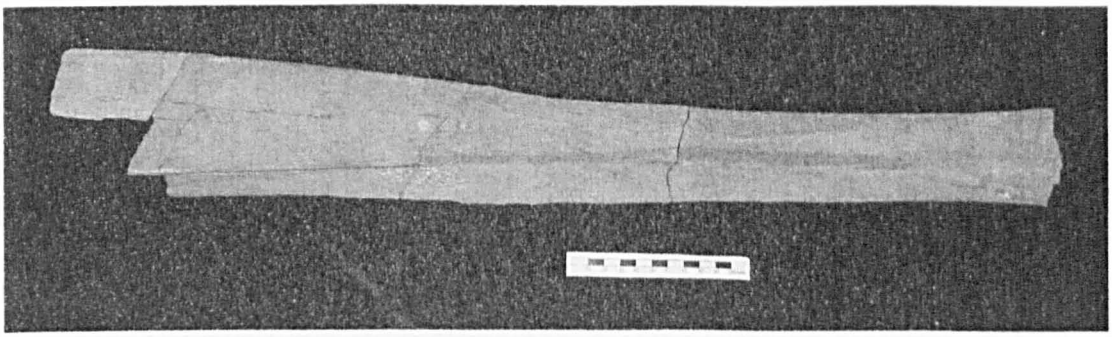


Figure 4.7. Ceratobranchial of *Leedsichthys*, part of the holotype specimen BMNH P.6921, in dorsal view. Scale bar = 100mm.

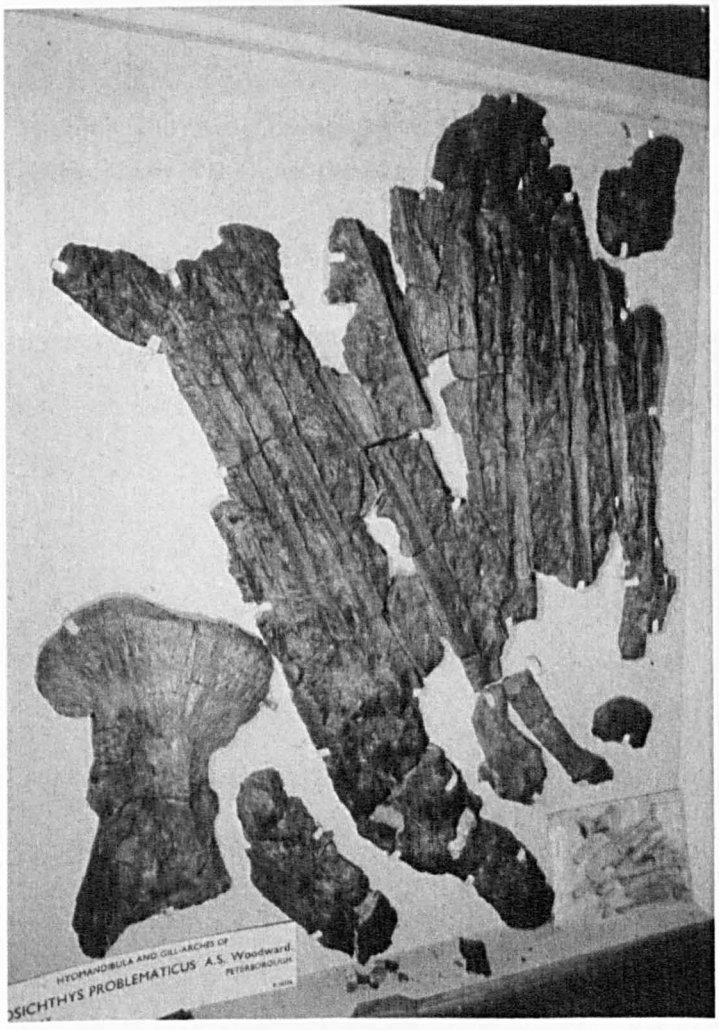


Figure 4.8. Gill basket specimen BMNH P.10156 on display in the 1970s. This specimen was excavated as a nodule by Alfred Leeds, and so preserves much of its three dimensional form without the crushing normally associated with English Oxford Clay specimens of *Leedsichthys*. The hyomandibula on the left is 687mm high.

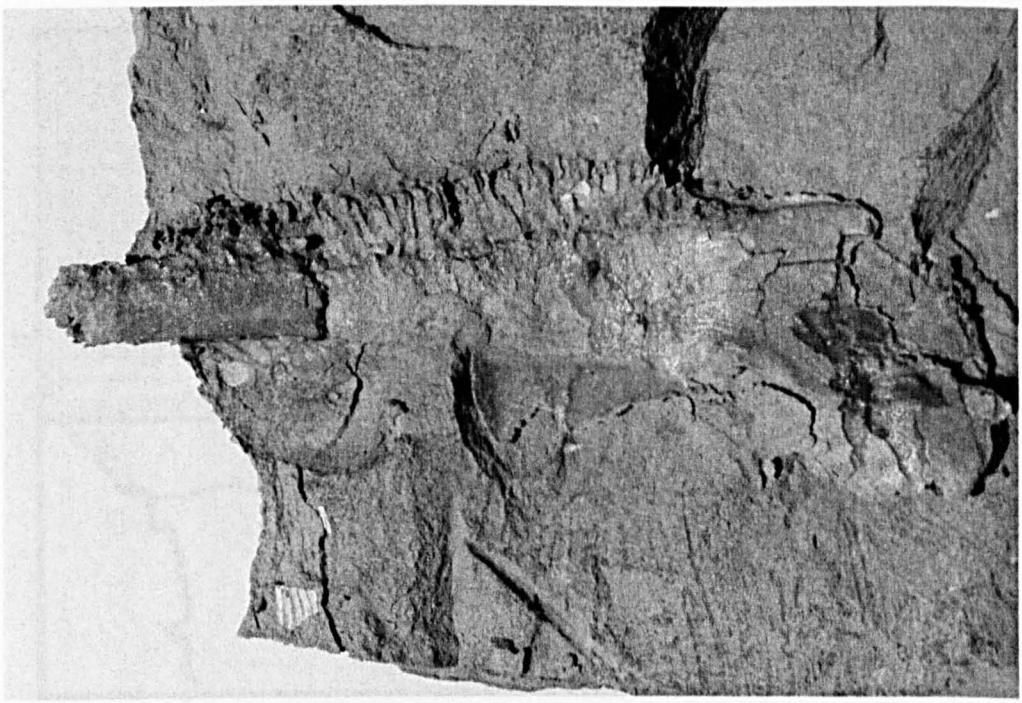


Figure 4.9. Gill raker of *Leedsichthys* (G.1073J) from the Upper Kimmeridgian of Cap de la Hève, image courtesy of D. Gielen. Gill raker is 73mm in length.

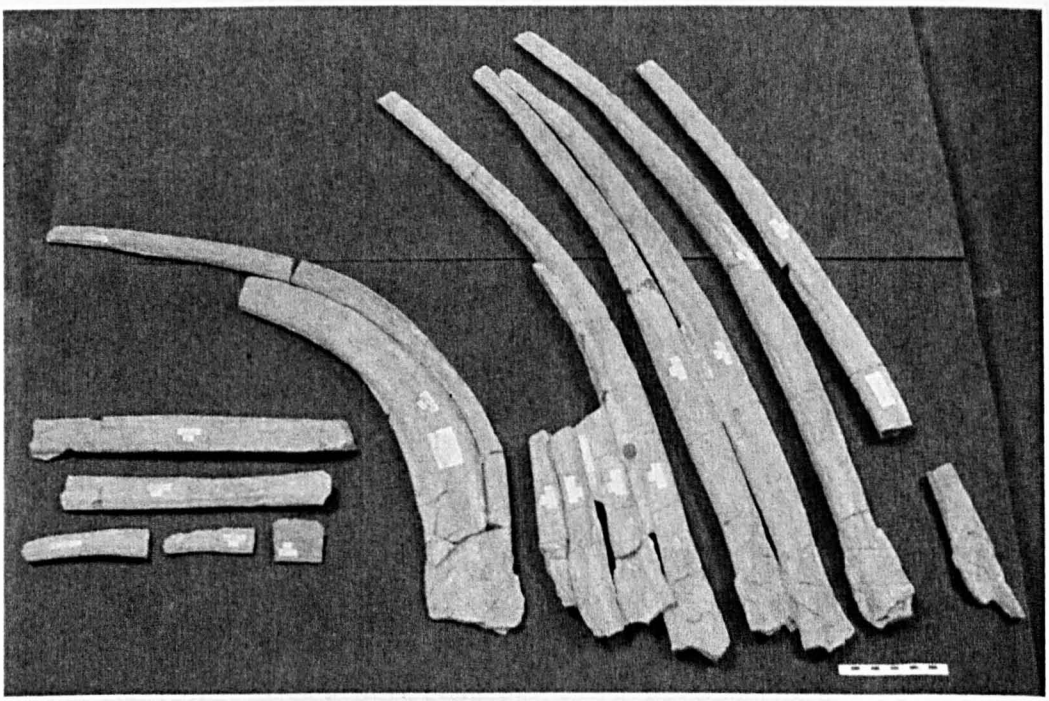


Figure 4.10. CAMSM J46873, the *Leedsichthys* remains figured as stegosaur 'Schwanzstacheln' by von Huene in 1901. Scale bar = 100mm.

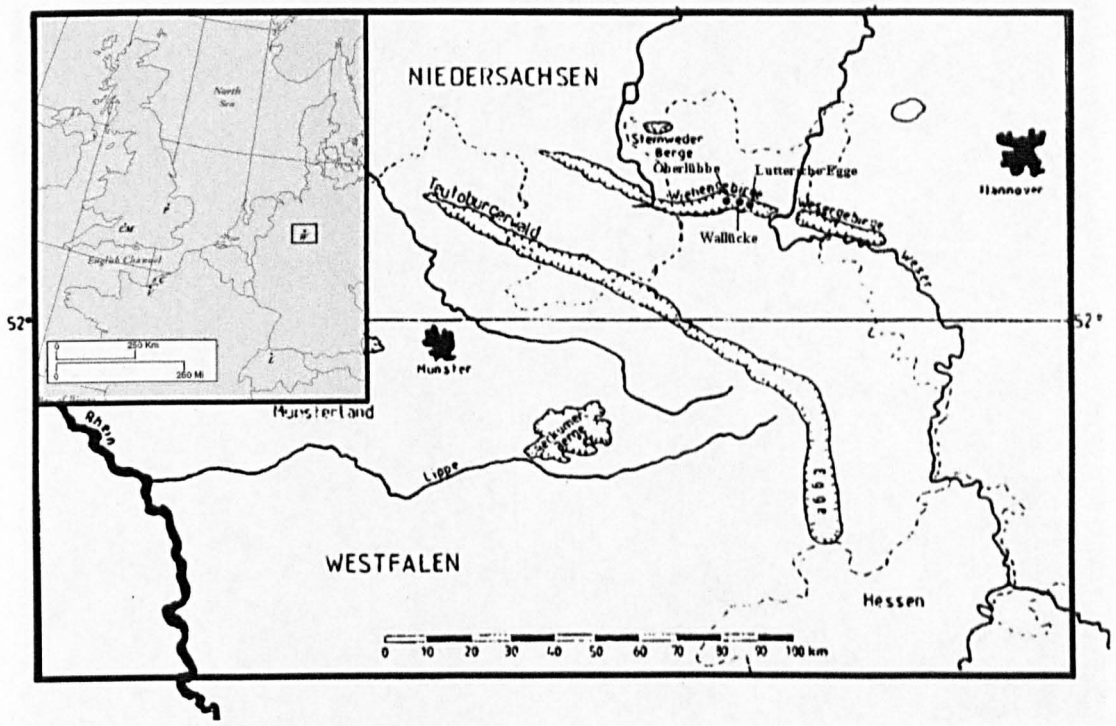


Figure 4.11. Map showing localities in the Wiehen Mountains in northern Germany, after Metzdorf.

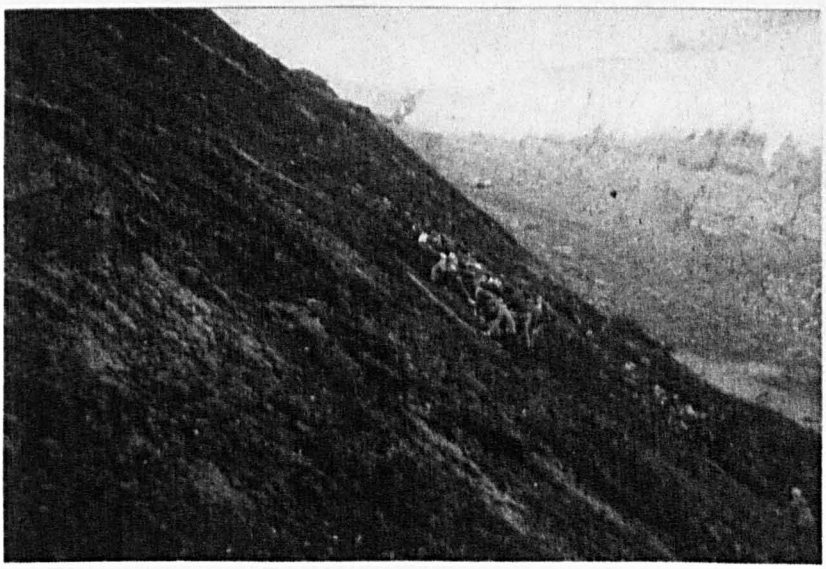


Figure 4.12. The November 1983 joint excavation in Wallücke. Image courtesy of R. Metzdorf.

Figure 4.13. Bones of *Leedsichthys* exposed next to a specimen of *Erymnoceras*, the ammonite that originally led the fossil collectors to prospect in the quarry. Brick hammer for scale. Image courtesy of R. Metzdorf.

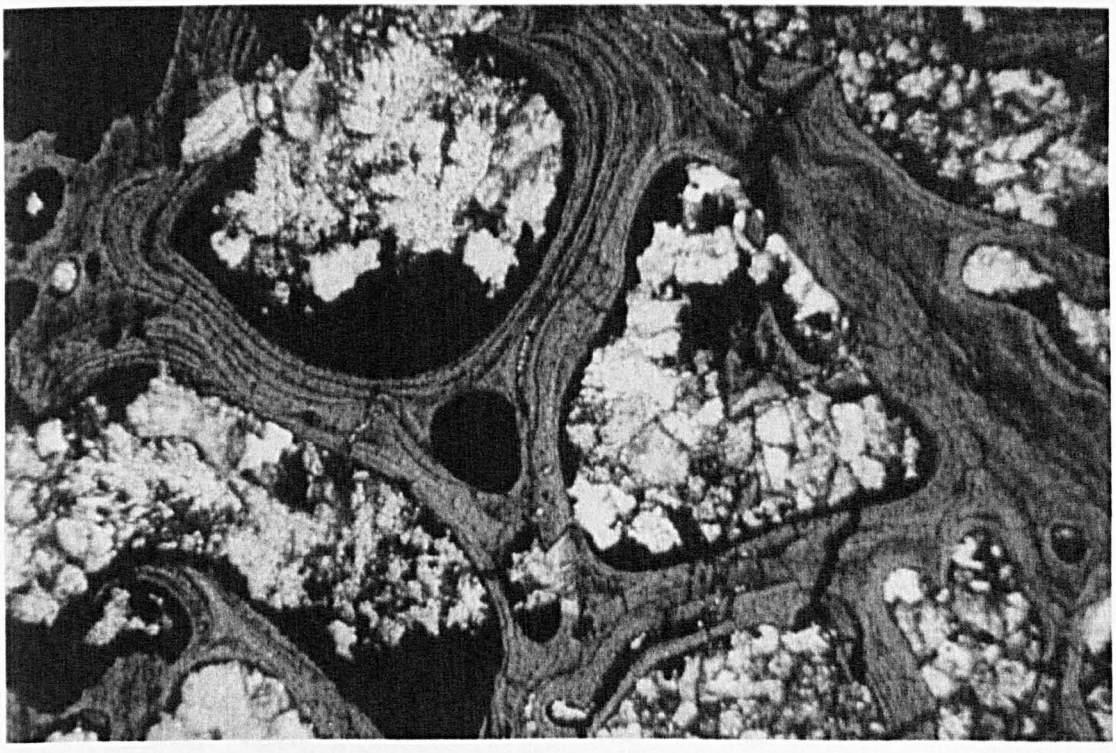


Figure 4.14. Transverse section of specimen by Büchner, showing no xylem and phloem vessels. Image courtesy of R. Metzdorf.

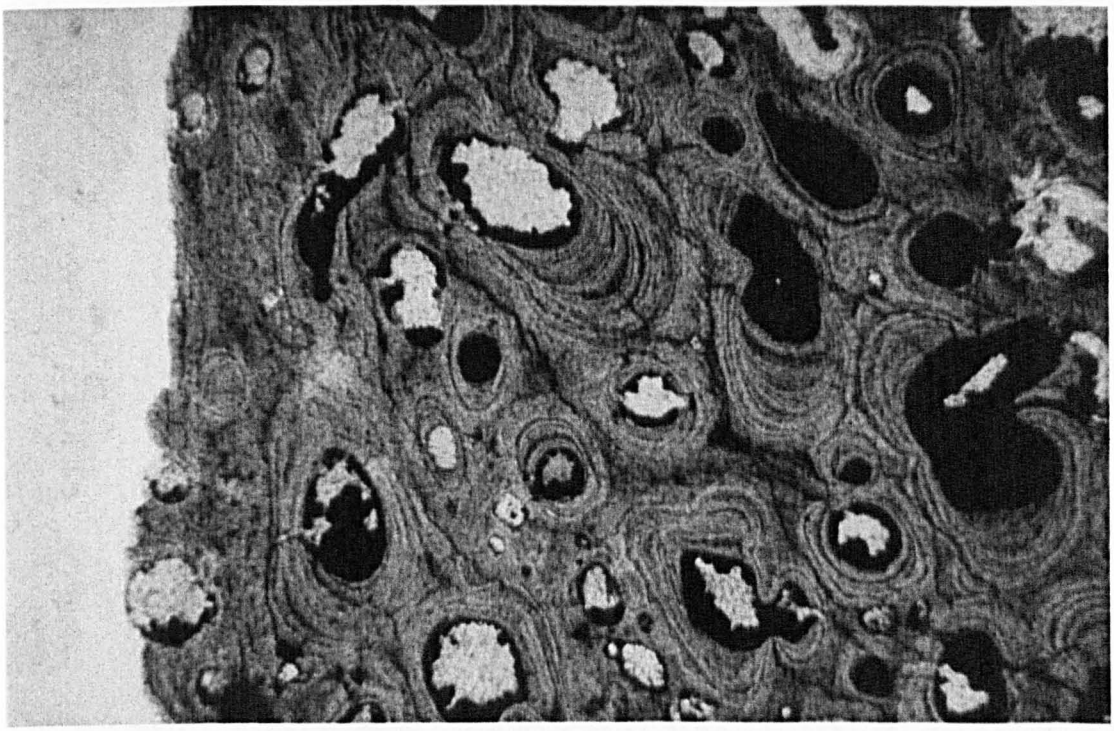


Figure 4.15. Transverse section of specimen by Büchner, showing no xylem and phloem vessels. Image courtesy of R. Metzdorf.

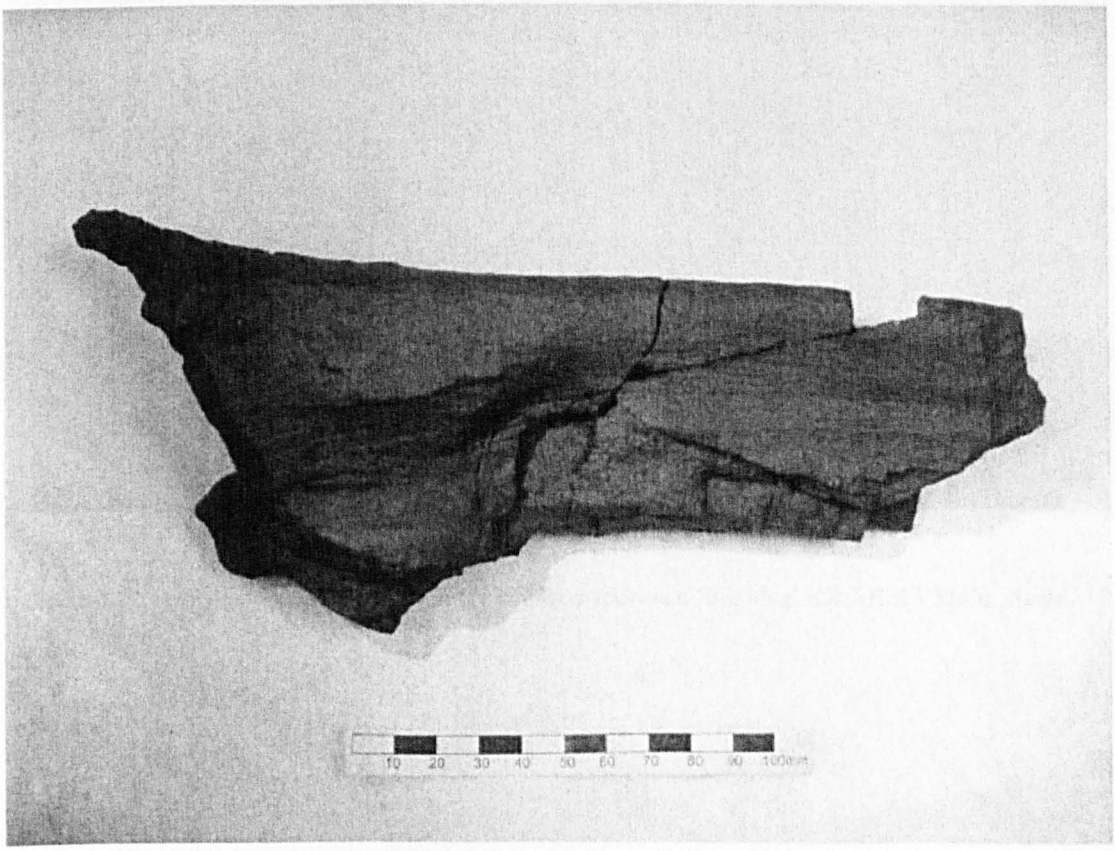


Figure 4.16. Hypobranchial of *Leedsichthys*. Cast (GLAHM 109508) of WMfN PM 17006/8. Scale bar = 100mm.

Figure 4.17. Hypobranchial (broken) from *Leedsichthys* specimen 'Big Meg' (GLAHM V3363). Scale bar = 50mm.

Figure 4.18. Hypobranchial from *Leedsichthys* specimen 'Ariston' (PETMG F174) indicated by black arrow. Boot in foreground for scale.

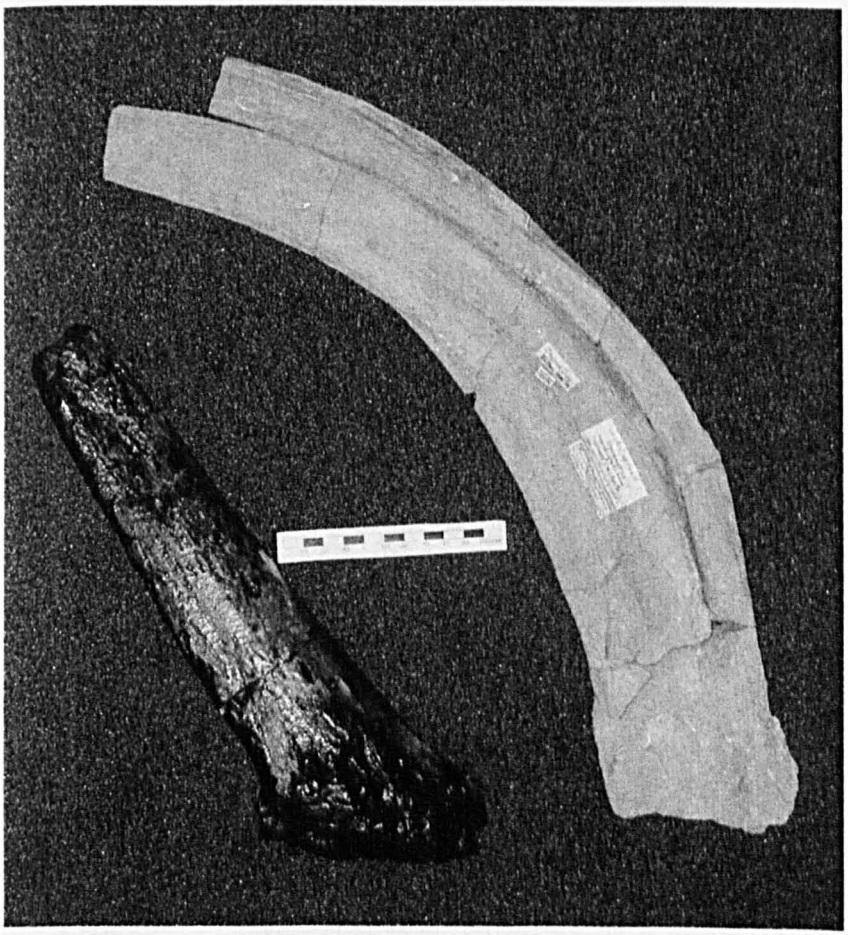


Figure 4.19. Tail-spine of *Lexovisaurus* (CAMSM J46879) with element from *Leedsichthys* series of dorsal fin-rays, figured by von Huene (CAMSM J46873). Scale bar = 100mm.

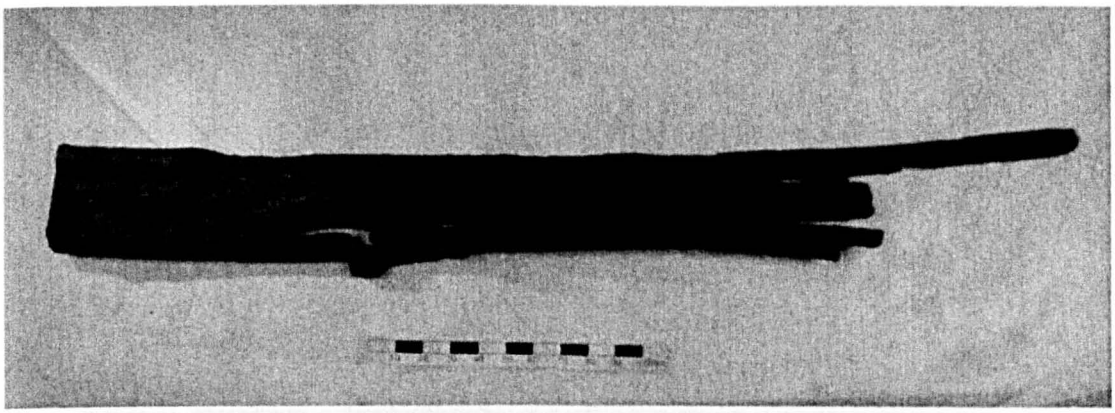


Figure 4.20. Cast (GLAHM 109509) of WMfN PM 17006/1, showing apparent tendons cross-linking between fin-rays. Scale bar = 100mm.

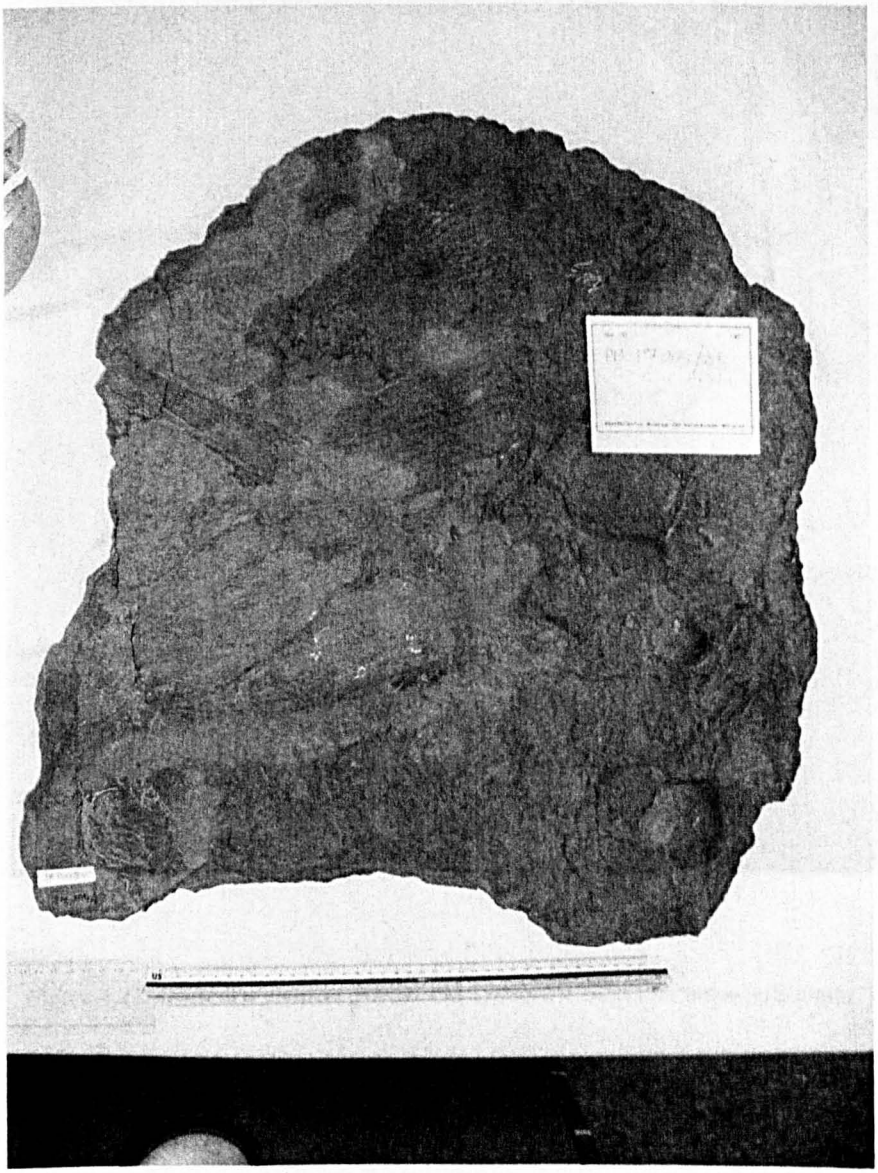


Figure 4.21. Skull roof element WMfN PM 17005/23. Scale bar below is 300mm.

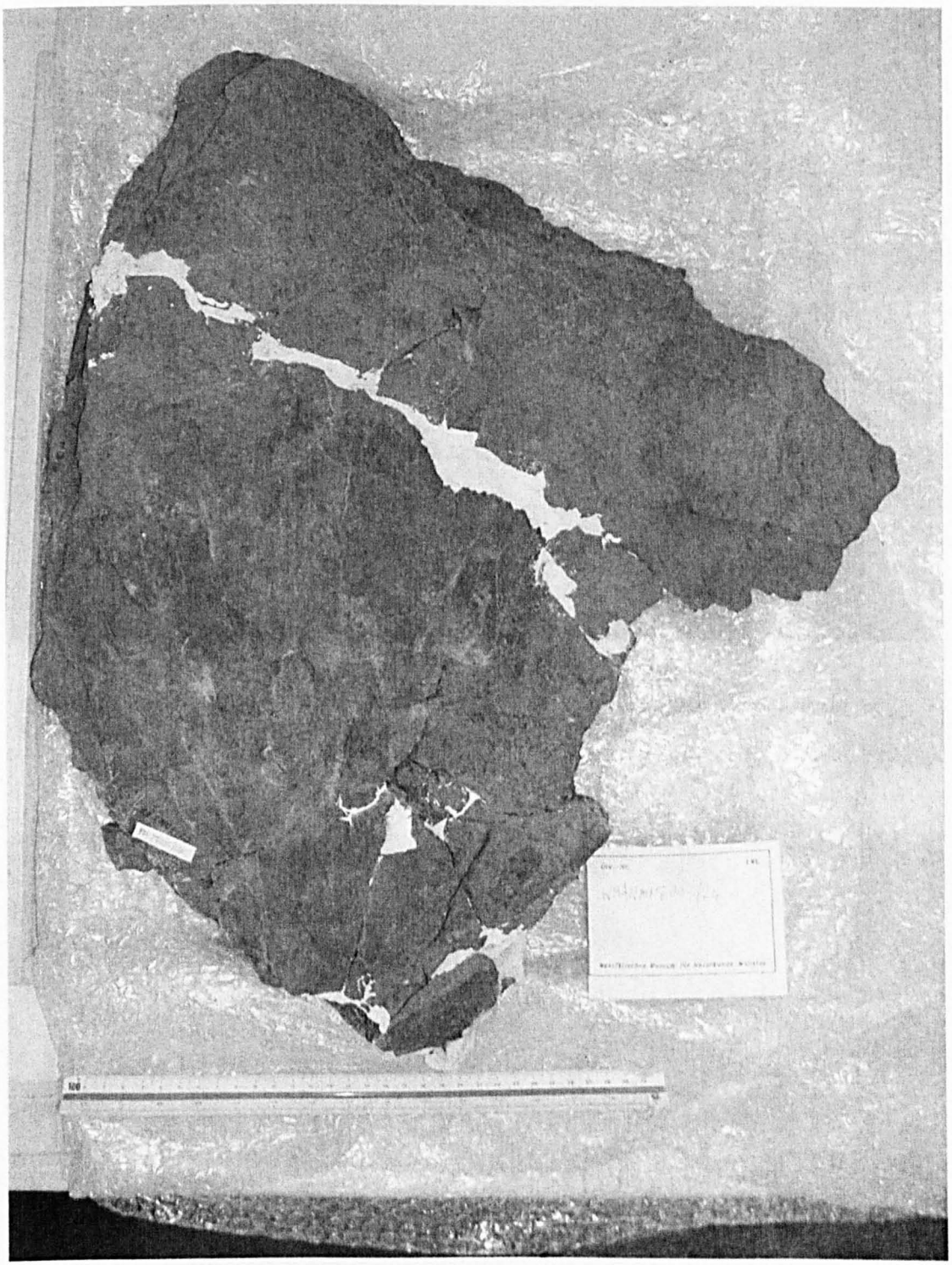


Figure 4.22. Opercular element WMfN PM 17005/24. Scale bar below is 300mm.

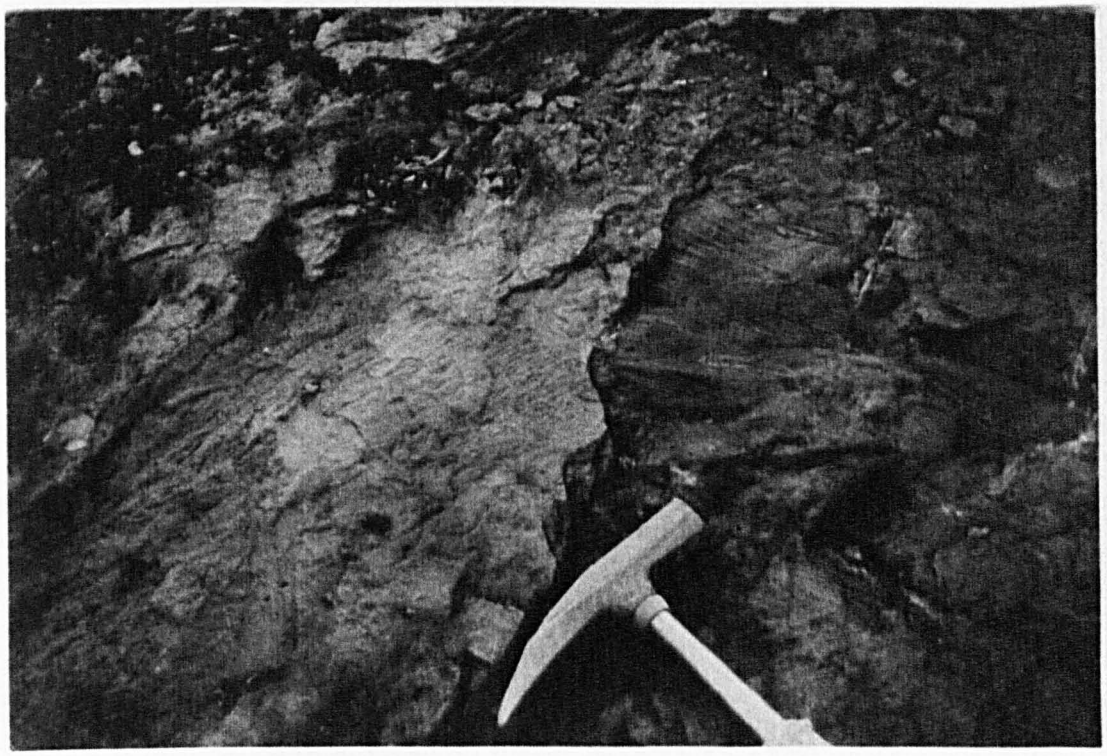


Figure 4.23. WMfN PM 17005/23 and WMfN PM 17005/24 as found in the field. Brick hammer for scale. Image courtesy of R. Metzdorf.

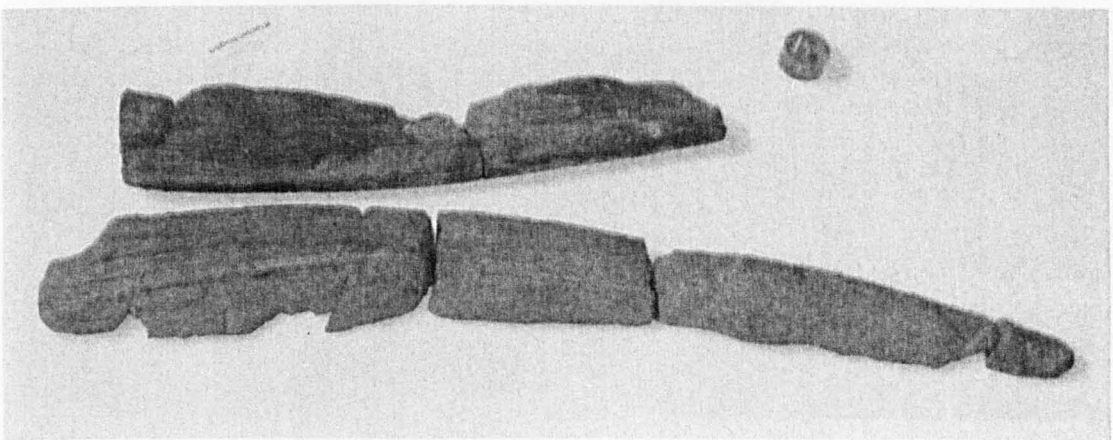


Figure 4.24. Specimen PHB W 138/4 (above) with PMM 19.1-21.1, 23.1. Resin cylinder in top right is 21mm in diameter.

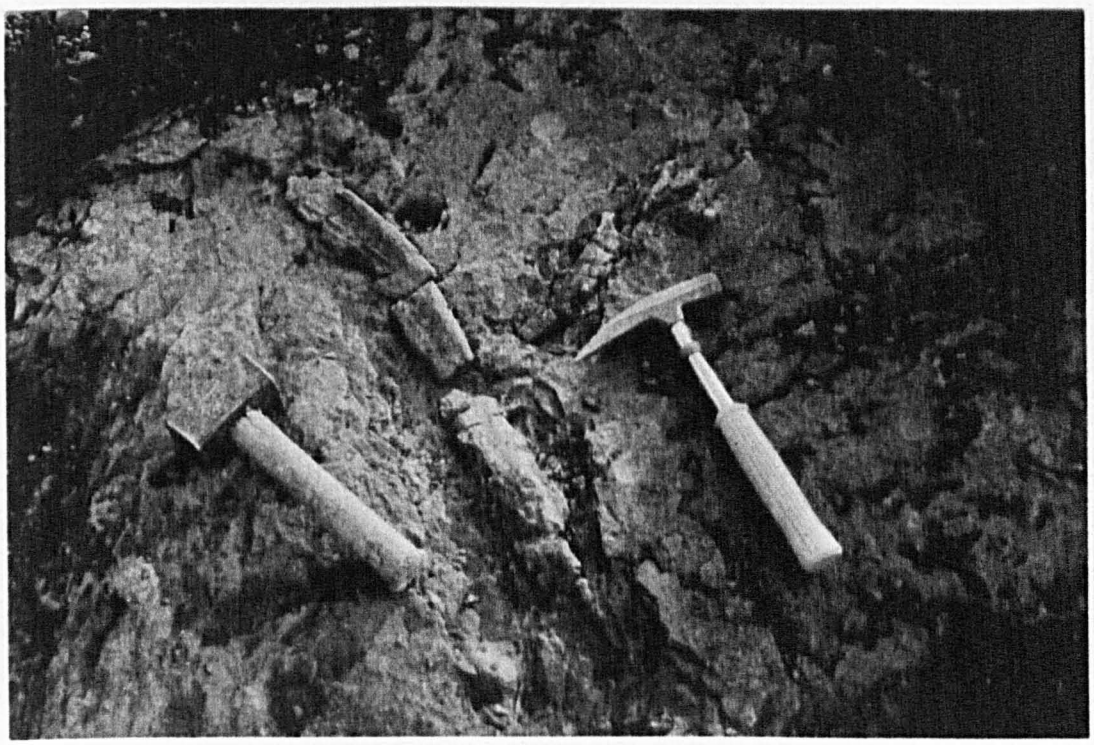


Figure 4.25. PMM 19.1-21.1, 23.1 as found in the field. Image courtesy of R. Metzdorf. Brick hammer for scale.

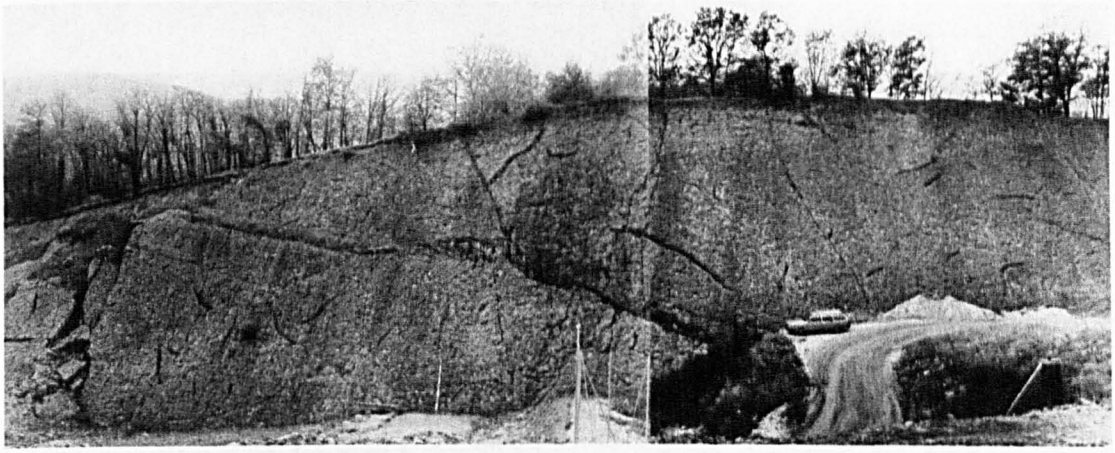


Figure 4.26. The Liesbergmüli clay pit in 1987, showing the range of alleged iliophagous 'gutter traces'. Note car to right of image for scale. Image courtesy of J. Geister.

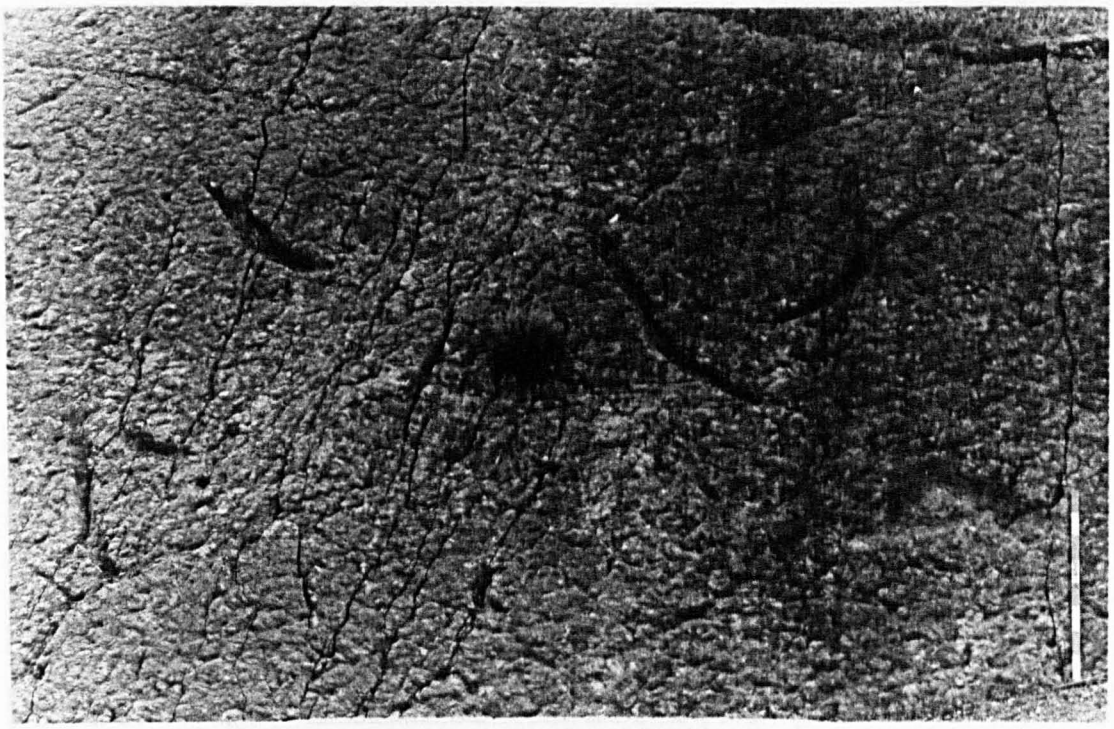


Figure 4.27. Some of the wider iliophagous 'gutter traces' originally argued to be made by pliosaurs . Groove to the upper left is 3.5 metres long and attains a maximum width of 60cm, groove to the right of centre of view is 5.5 metres long and 45cm wide. Image courtesy of J. Geister.

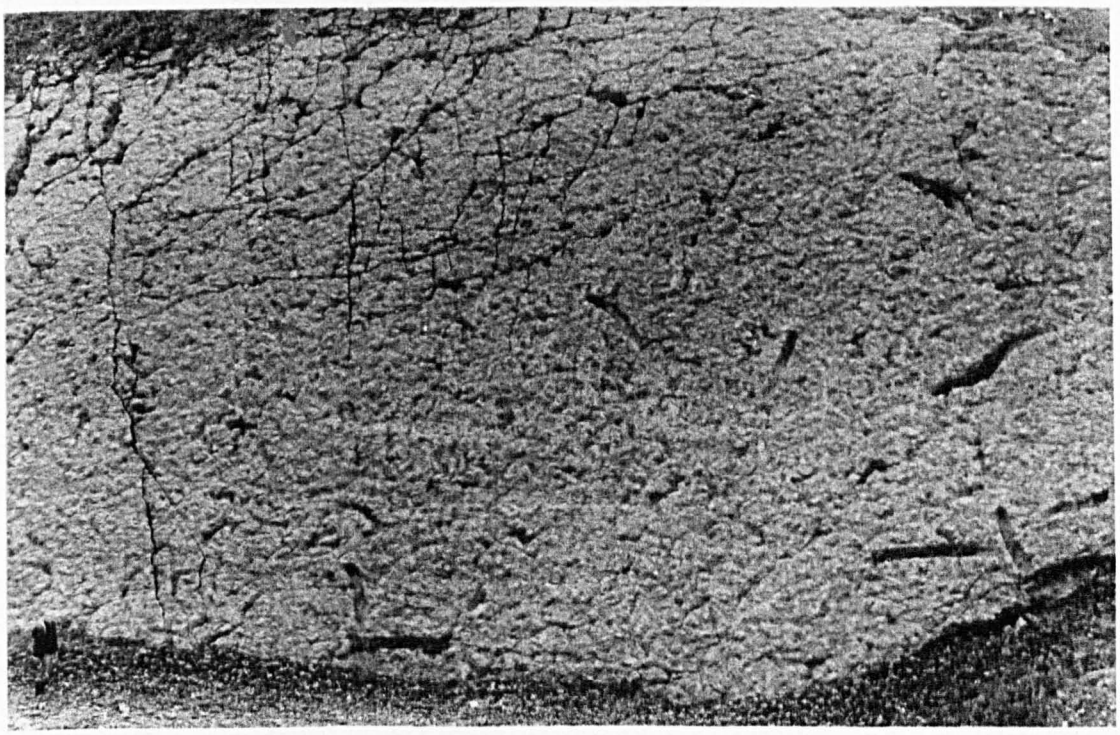


Figure 4.28. Broader view of bed, showing disposition of range of sizes of putative traces of benthic feeding (for scale, note figure, 1.8 metres high, in bottom left of photograph). Image courtesy of J. Geister.

Figure 4.29. Map of Chile, showing Antofagasta and the 1994 and 1999 localities: S = Quebrada del Profeta, M = Quebrada Corral.

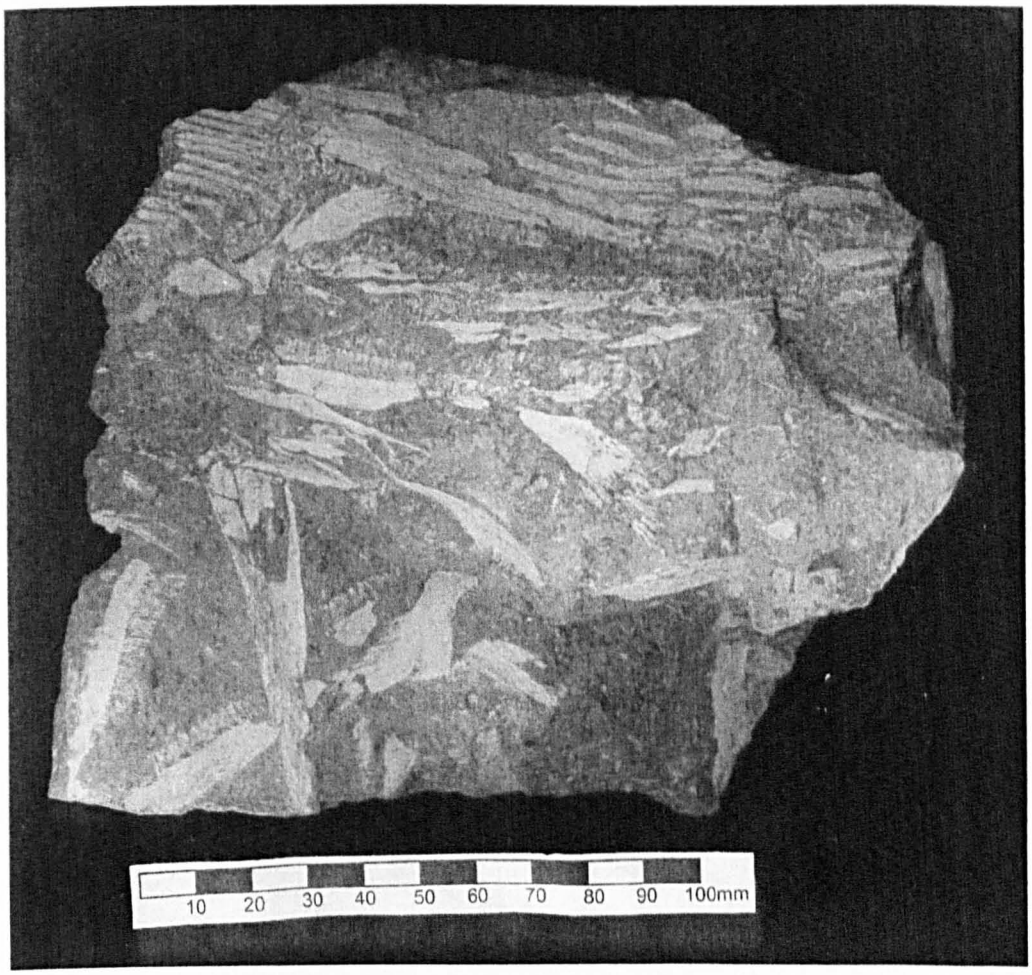


Figure 4.30. I-190173, a specimen collected from east of Antofagasta. Scale bar = 100mm.

Figure 4.31. I8-021173, a specimen collected from east of Antofagasta. Scale bar = 100mm.

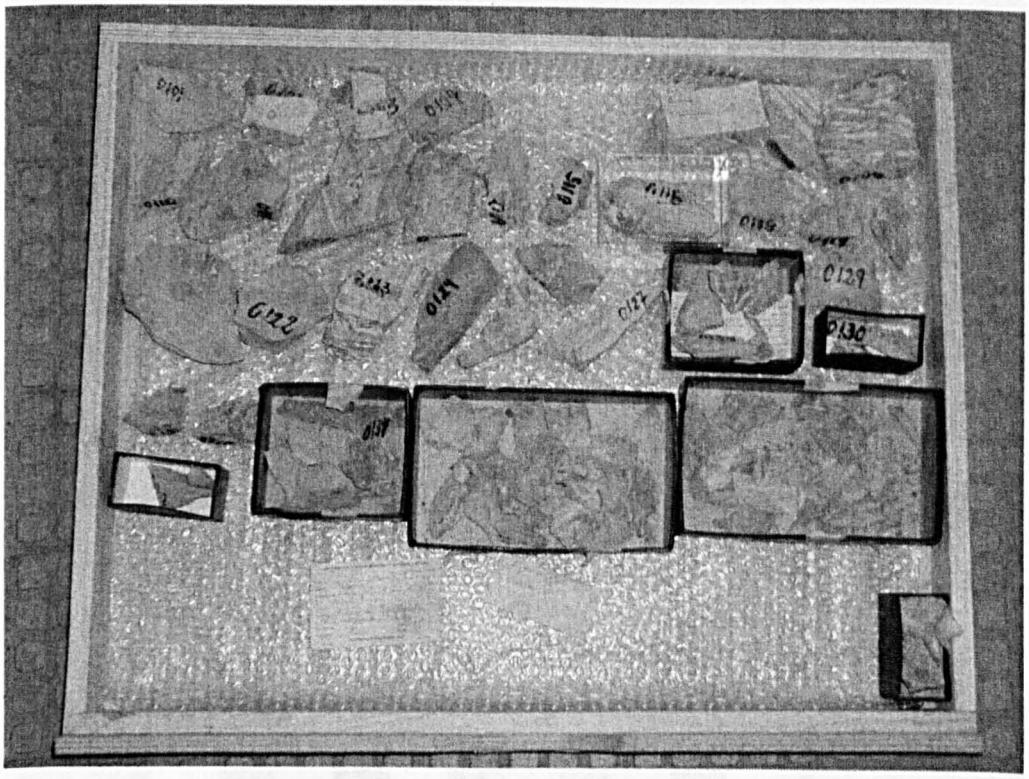


Figure 4.32. Some of the material collected in 1978 by H.-P.Schultze. Drawer is 500mm wide.

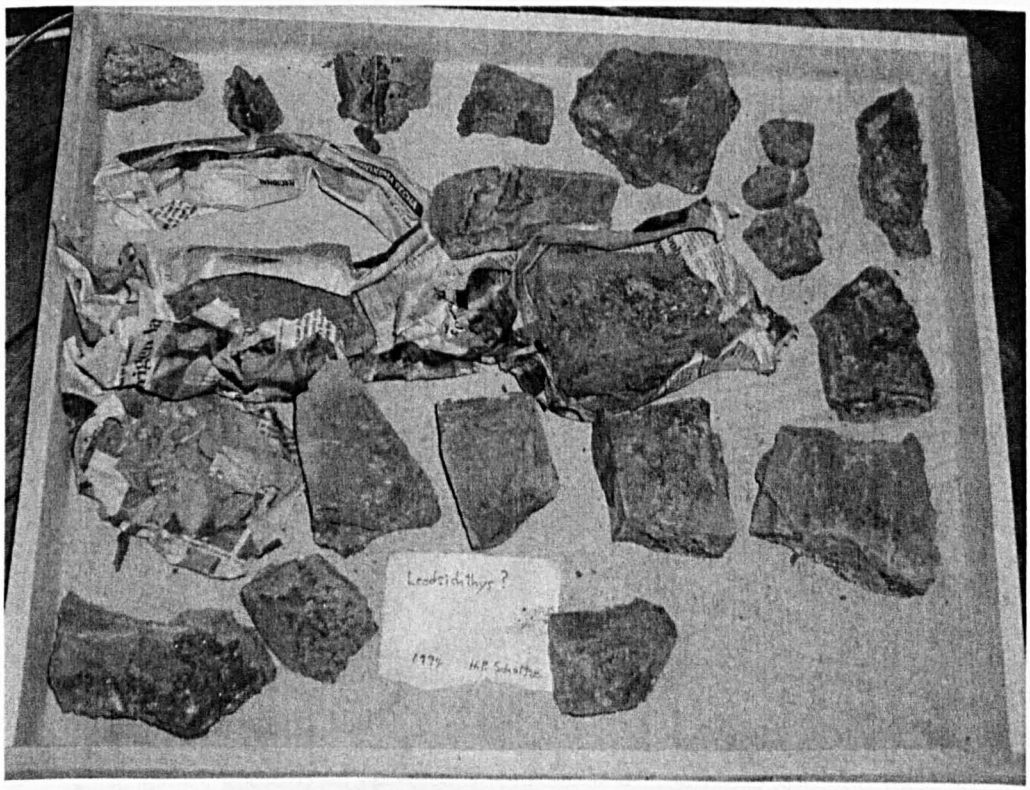


Figure 4.33. Some of the material collected in 1994 by H.-P.Schultze. Drawer is 500mm wide.

Figure 4.34. Type specimen (SMNK 2573 PAL) of *Leedsichthys notocetes*. Scale bar = 100mm.

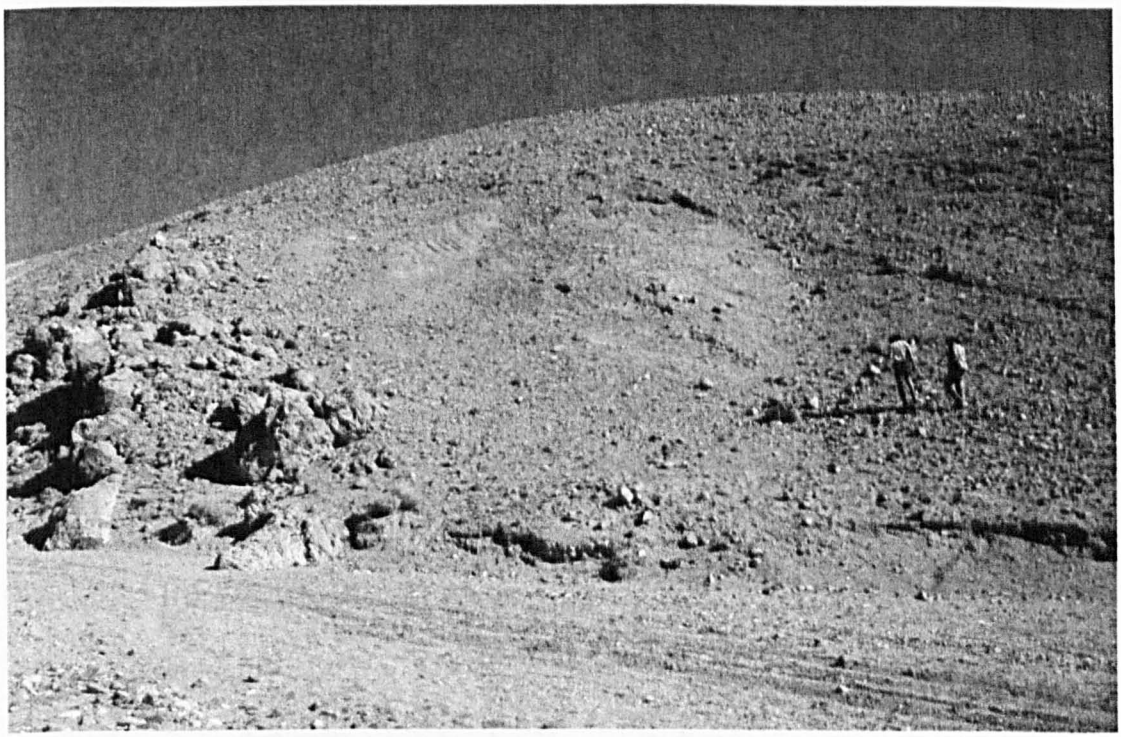


Figure 4.35. Type locality of *Leedsichthys notocetes*, with Frey (figure on left, 1.8m tall) for scale.

Chapter 4: Tables

Table 4.1. Details of *Leedsichthys* specimens from various localities

Specimen number	Collector/collection	Date Collected	Locality	Description
G.1073	D. Gielen	2004	Cap de la Hève, Normandie	single gill raker plus many lepidotrichia
private	G. & E. Pennettier	1980s-1990s	Vaches Noire, Normandie	gill rakers plus ceratobranchial elements
BMNH 32581	Tesson of Caen	1857	Vaches Noire, Normandie	cluster of disarticulated gill rakers
WMfN PM 17006/8	Westfalisches Museum	July 1982-November 1983	Wallücke	hypobranchial
WMfN PM 17006/1	Westfalisches Museum	July 1982-November 1983	Wallücke	(?caudal) fin-rays with possible traces of tendons
WMfN PM 17005/2	Westfalisches Museum	July 1982-November 1983	Wallücke	distal extremities of 2 ?dorsal fin-rays
WMfN PM 17005/23	Westfalisches Museum	July 1982-November 1983	Wallücke	piece with texture like crest of hyomandibula or edge of parietal
WMfN PM 17005/24	Westfalisches Museum	July 1982-November 1983	Wallücke	possible opercular series of plates
PHB W 138/4	Breitkreutz	July 1982-November 1983	Wallücke	?left cleithral fragment
PMM 19.1-21.1, 23.1	Metz	July 1982-November 1983	Wallücke	?supraangular
GLAHM 109518	Hunterian Museum	Jul-02	Wallücke	isolated ray fragments
BMNH P.6921	Alfred N. Leeds	pre-1887	Peterborough district	holotype specimen: dorsal, pectoral and caudal fin-rays, skull etc.
BMNH P.6922	Alfred N. Leeds	pre-1887	Peterborough district	preopercle plus two fragments
BMNH P.10000	Alfred N. Leeds	March 1898	Peterborough district	skull material with gill rakers, cleithra, parasphenoid and tail
BMNH P.10156	Alfred N. Leeds	Jul-05	Peterborough district	articulated gill basket with left hyomandibula, ?supraangular
BMNH P.66340	Alfred N. Leeds	pre-1919	Peterborough district	primarily jaw elements, including right dentary, ?supraangular
BMNH 46355	William Cunnington	1875	Christian Malford, Wiltshire	isolated ray fragment
PETMG F.174	Peterborough Museum	2001-2003	Whittlesey, Peterborough	skull, fin and gill raker material
CAMSM J.46873	Henry Keeping	1898	Fletton, Peterborough	dorsal fin-rays
SMNK 2573.PAL	Karlsruhe Museum	1998	Quebrada Corral, Chile	disarticulated gill rakers
I-190173	Museo de Arqueologia, Antofagasta	Jan-73	east of Antofagasta	disarticulated gill rakers
I8-021173	Museo de Arqueologia, Antofagasta	Nov-73	east of Antofagasta	articulated series of gill rakers
(unnumbered)	Museo Nacional de Historia Natural, Santiago	1994	Quebrada del Profeta, Chile	gill rakers plus unprepared material

Chapter 5: Figures

Figure 5.1. BMNH P.61563 *in situ* in Dogsthorpe Pit in 1983, prior to recovery. Collage from images supplied by Alison Longbottom, NHM (London). Lens cap at right 60 mm in diameter, total length of specimen = 2305 mm.

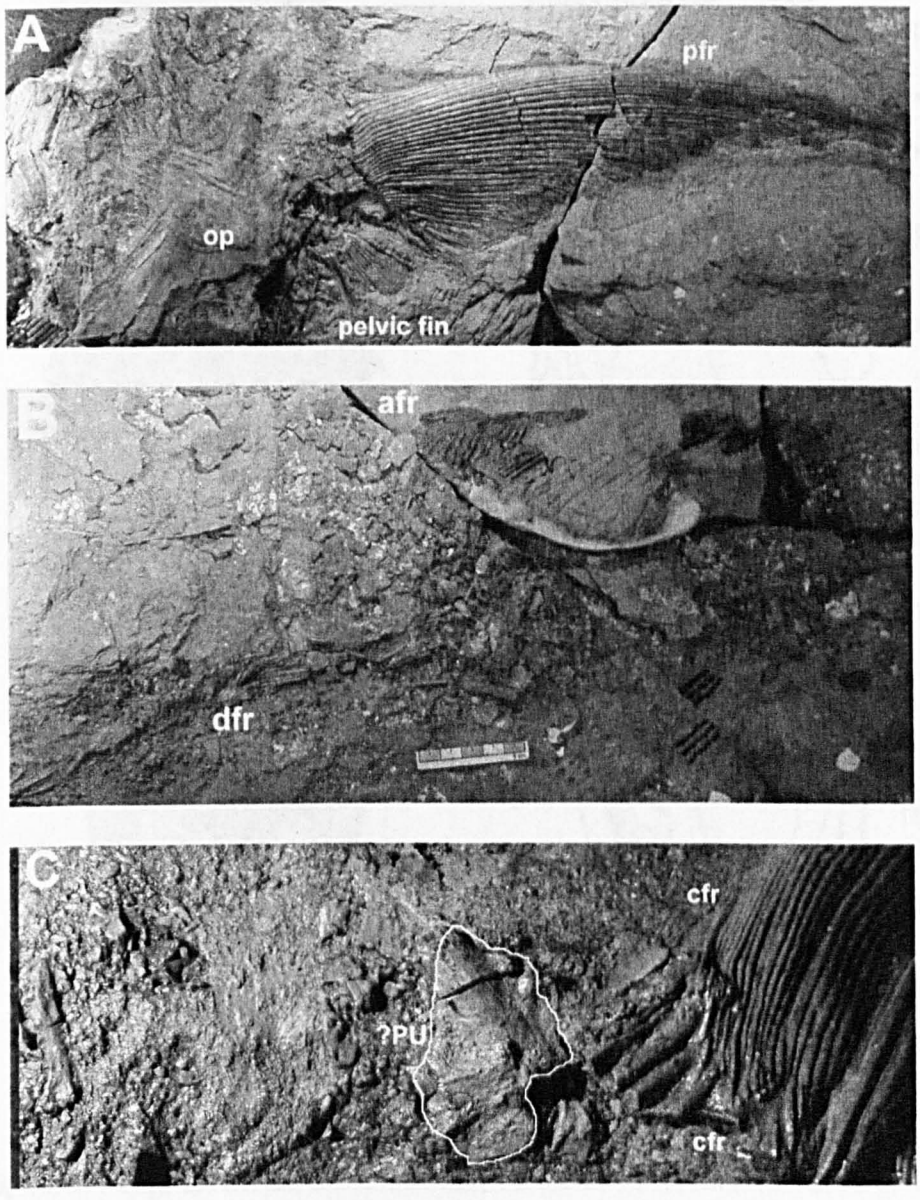


Figure 5.2. Fins of BMNH P.61563. **A**. Right pectoral and pelvic. Pectoral fin 244 mm long. **B**. Dorsal (47 mm base) and anal (17 mm base). Scale bar = 50 mm. **C**. Caudal lobes. ?Preural = 18 mm breadth. Abbreviations: **afr,** anal fin rays; **cfr,** caudal fin rays; **dfr,** dorsal fin rays; **op,** fragments of right opercular bones; **pfr,** pectoral fin rays; **?PU,** possible first preural vertebra.

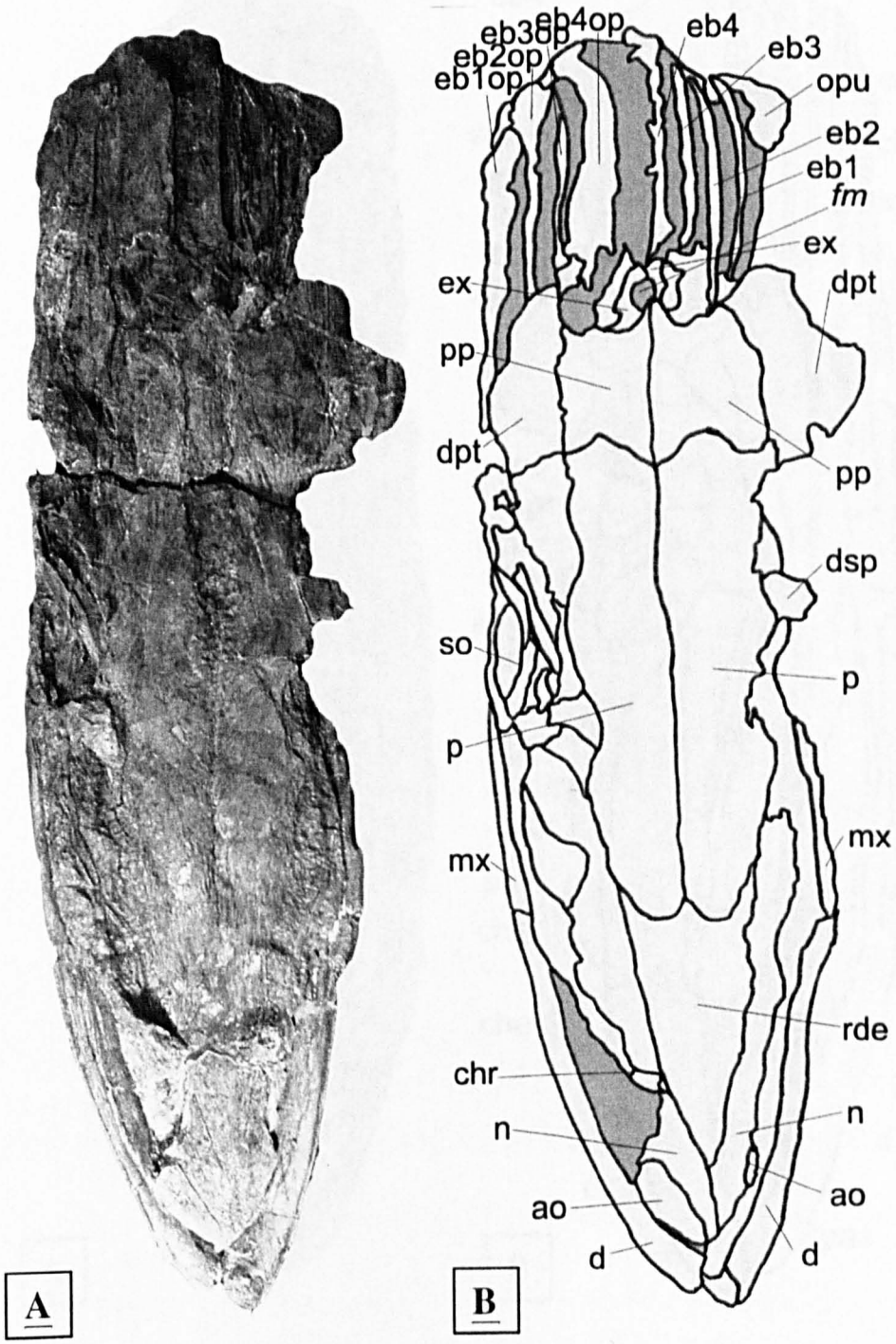


Figure 5.3. Photograph (**A**) and outline drawing (**B**) of dorsal view of skull of BMNH P.61563. Length of skull = 370 mm. Abbreviations: **ao,** antorbital; **chr,** area where right ceratohyal has been displaced through the skull roof; **d,** dentary; **dpt,** dermopterotic; **dsp,** dermosphenotic; **eb1-4,** left epibranchials 1-4; **eb1-4op,** right epibranchials overlain by right opercle; **ex,** exoccipital; **fm,** foramen magnum; **mx,** maxilla; **n,** nasal; **opu,** inner surface of left opercle; **pp,** parietal; **rde,** rostrodermethmoid; **so,** supraorbitals.

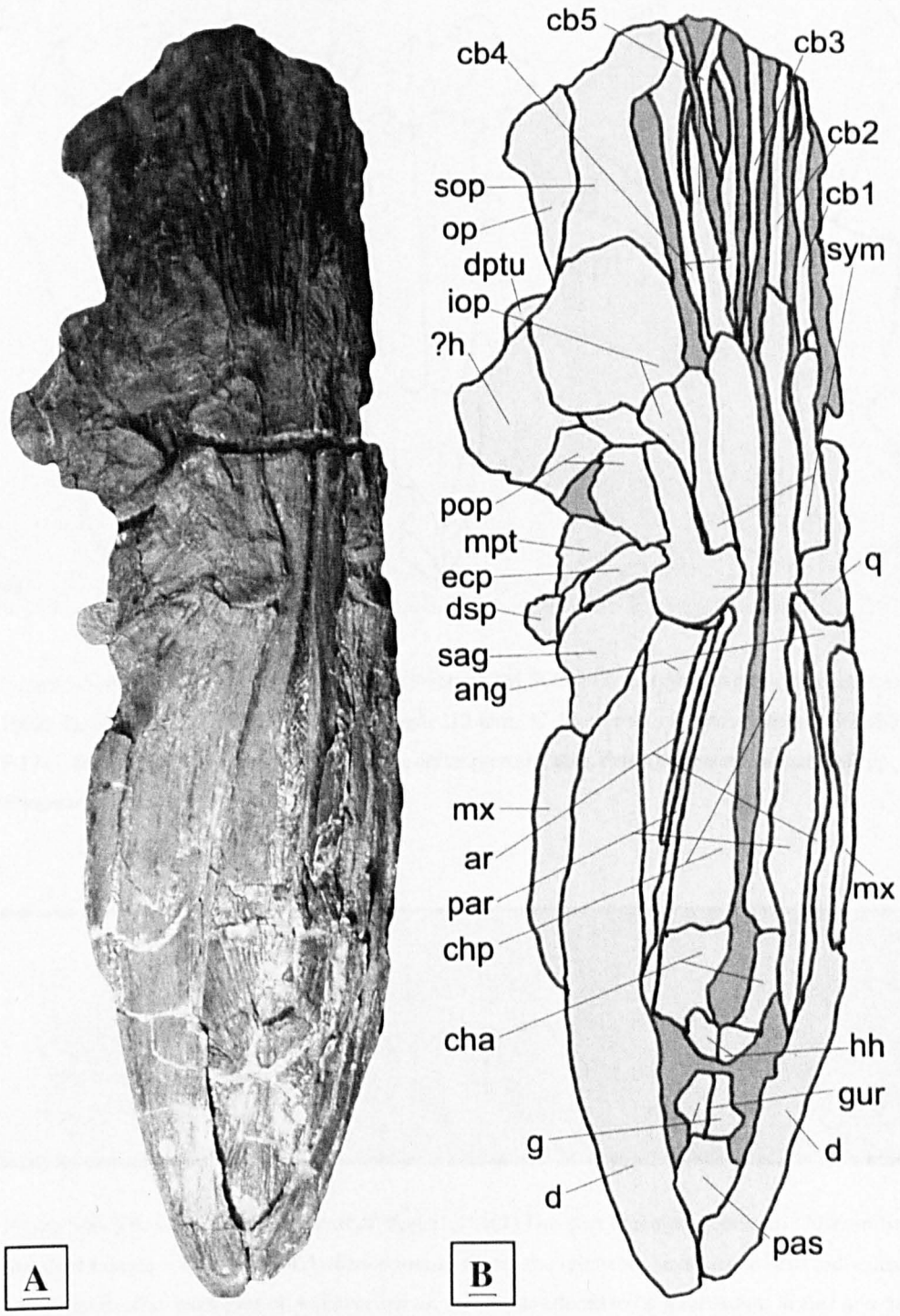


Figure 5.4. Photograph (**A**) and outline drawing (**B**) of ventral view of skull of BMNH P.61563. Length of skull = 370 mm. Abbreviations: **ang,** angular; **ar,** articular; **cb1-5,** ceratobranchials 1-5; **cha,** anterior ceratohyal; **chp,** posterior ceratohyal; **d,** dentary; **dsp,** dermosphenotic; **dptu,** inferior surface of dermopterotic; **ecp,** ectopterygoid; **g,** gular; **gur,** ventral gular ridge; **?h,** possible fragment of hyomandibula; **hh,** hypohyal; **iop,** interopercle; **mpt,** metapterygoid; **mx,** maxilla; **op,** opercle; **par,** prearticular; **pas,** parasphenoid; **pop,** preopercle; **q,** quadrate; **sag,** supraangular; **sop,** subopercle; **sym,** symplectic.

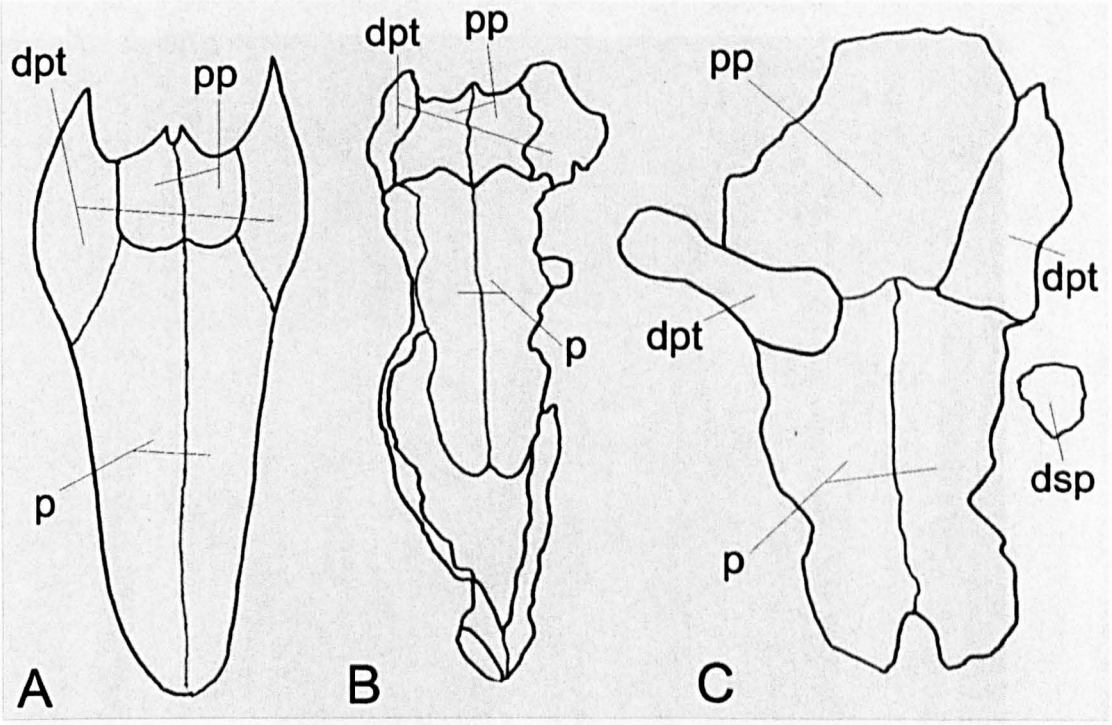


Figure 5.5. **A**. Skull roof of *Asthenocormus* (Neotype JM SOS 542), length 264 mm (after Lambers 1992). **B**. Skull roof of BMNH P.61563, length 212 mm. **C**. Skull roof of *Leedsichthys* (PETMG F.174), length 918 mm. Abbreviations: **dpt,** dermopterotic; **dsp,** dermosphenotic; **p,** parietal; **pp,** postparietal.

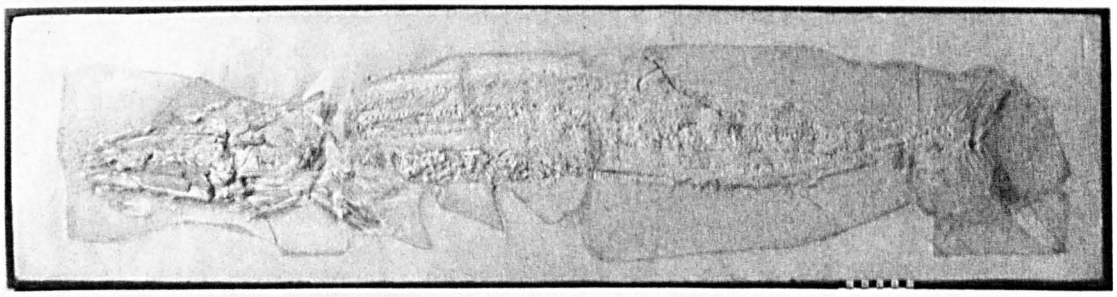


Figure 5.6. The surviving counterpart of Vetter's (1881) Dresden specimen (Dresden Museum BaJ2344, Standard Length = 1176 mm) of *Asthenocormus*. Given the relatively small size of this individual compared to other examples of *Asthenocormus*, this is considered to be a sub-adult. Scale bar = 100 mm.

Figure 5.7. The gill basket of BMNH P.10156 on display in the fossil fish gallery of the British Museum (Natural History) in 1924. Image supplied by Alison Longbottom, NHM (London). 300mm ruler sits in bottom of case for scale.

Figure 5.8. The reconstructed gill basket of *Leedsichthys* BMNH P.10156. Ventral view. Scale bar in centre = 200 mm. Abbreviations for 5.8-5.11: **bb,** basibranchial; **cbl1-3,** left ceratobranchials 1-3; **cbl4,** left fourth ceratobranchial; **cbr1-3,** right ceratobranchials 1-3; **cbr4,** right fourth ceratobranchial; **cb5,** fused fifth ceratobranchial; **chl,** fragments of left ceratohyal overlying matrix around branchial elements; **?eb,** possible epibranchial element or fragment of preopercle; **hbl,** left first and second hypobranchials; **hbl1,** left first hypobranchial; **hbl2,** left second hypobranchial; **br2,** right second hypobranchial; **lh,** left hypohyal; **rh,** right hypohyal.

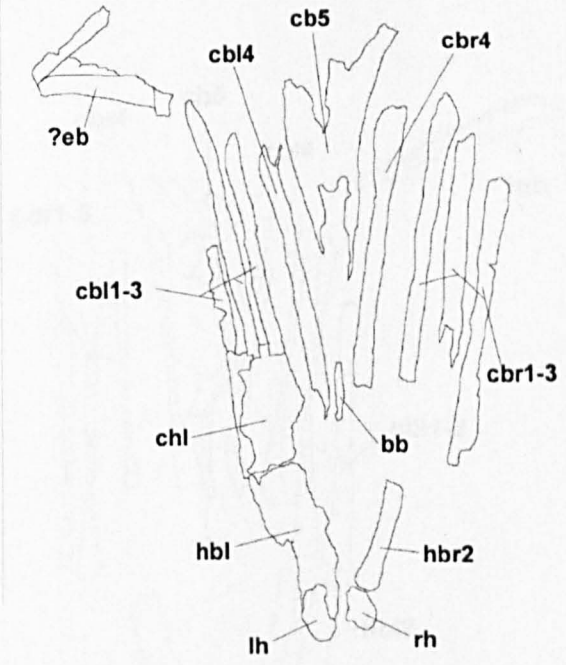


Figure 5.9. The reconstructed gill basket of *Leedsichthys* BMNH P.10156. Outline drawing of ventral view.

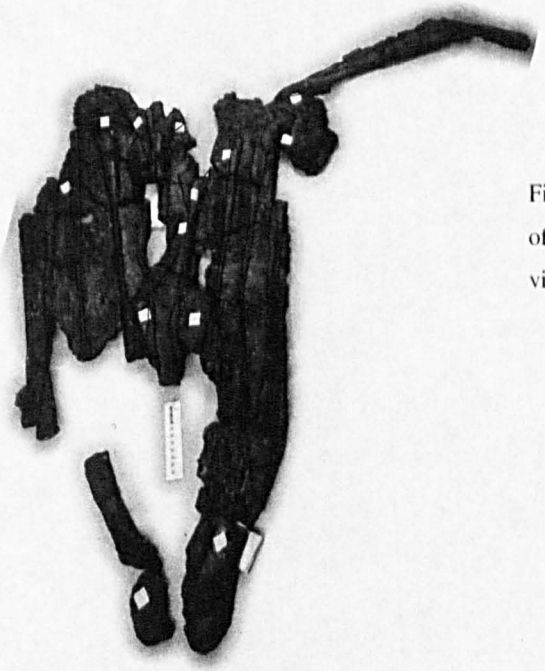


Figure 5.10. The reconstructed gill basket of *Leedsichthys* BMNH P.10156. Dorsal view. Scale bar in centre = 200 mm.

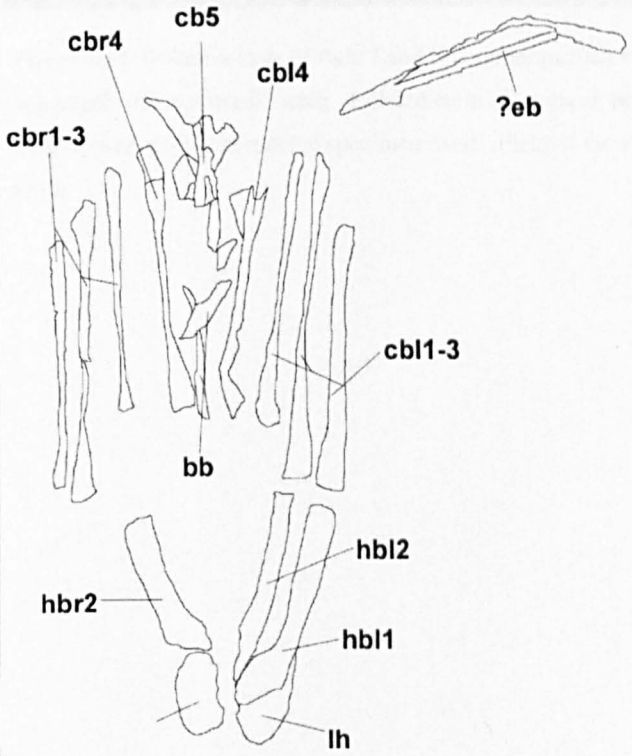


Figure 5.11. The reconstructed gill basket of *Leedsichthys* BMNH P.10156. Outline drawing of dorsal view.

Figure 5.12. Posterior ends of right I and II ceratobranchials of BMNH P.61563. Note gill rakers, apparently without needle teeth. Isolated teeth are present, but it seems more likely that they have come from scavengers than from the specimen itself. Field of view = 25 mm. Abbreviations: **gr,** gill raker; **t,** tooth.

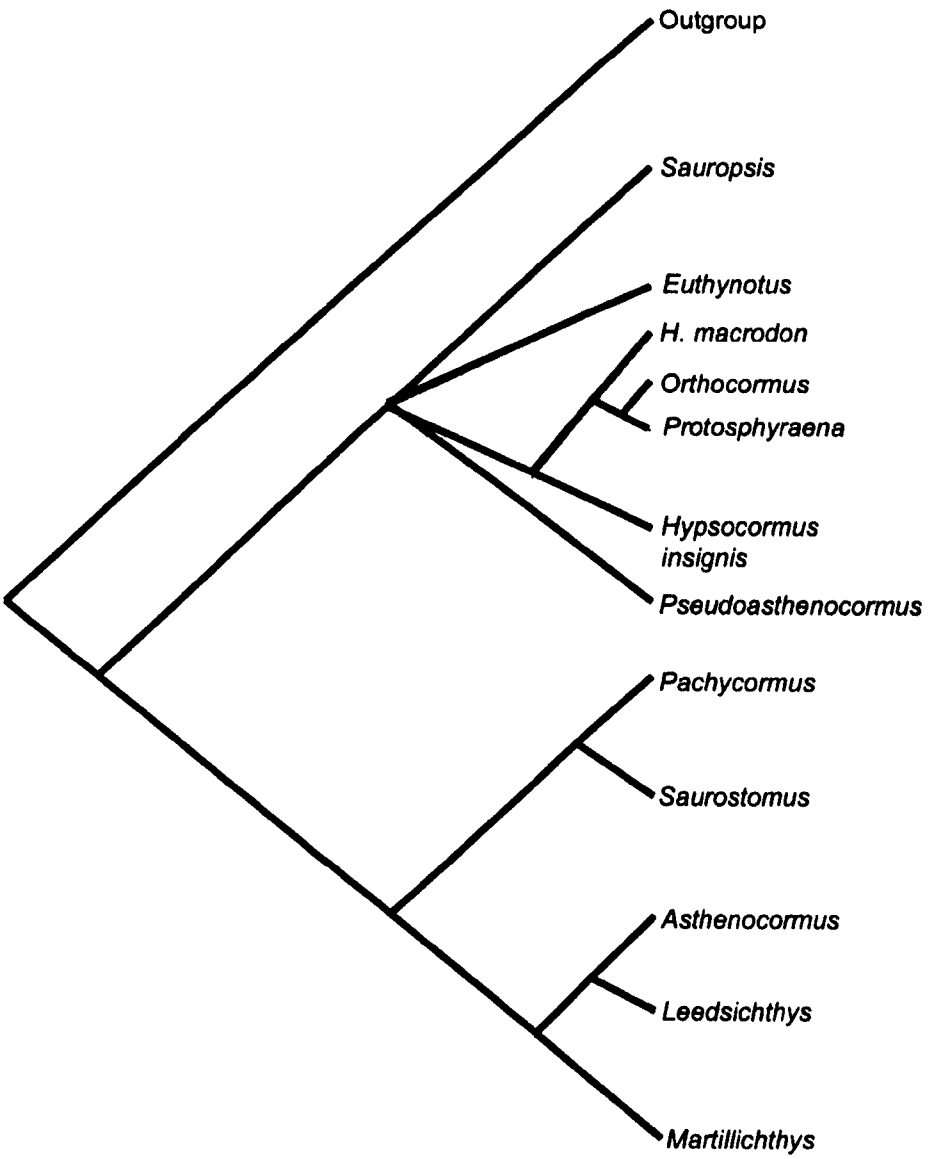


Figure 5.13. Strict consensus of five equally parsimonious trees based on fifteen unordered parsimony-informative characters.

Chapter 5: Tables

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Outgroup	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sauropsis	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	1
Euthynotus	0	0	0	0	1	0	0	0	1	0	0	1	0	0	0	1
Hypsocormus macrodon	0	1	1	1	0	1	0	2	1	0	1	1	0	0	1	1
Orthocormus	1	1	1	1	1	1	0	2	0	0	1	1	0	0	1	1
Hypsocormus insignis	0	1	0	0	0	1	0	1	0	0	0	1	0	0	1	1
Pseudoasthenocormus	0	0	0	0	1	1	0	1	1	0	0	1	0	0	1	1
Protosphyraena	1	1	1	1	1	1	0	1	?	?	?	?	1	?	1	1
Pachycormus	0	0	0	0	0	0	0	1	0	1	2	0	0	1	0	1
Saurostomus	0	0	0	0	0	1	0	1	0	1	2	0	0	1	1	1
Asthenocormus	0	2	2	2	2	2	1	0	0	?	2	0	1	0	?	1
Leedsichthys	?	?	?	?	2	2	1	1	?	1	2	0	1	1	1	1
Martillichthys	0	2	?	?	2	2	0	0	0	0	2	0	1	0	1	1

Table 5.1. Distribution of derived character states among the Pachycormidae. Dataset modified after Lambers (1992).

Chapter 6: Figures

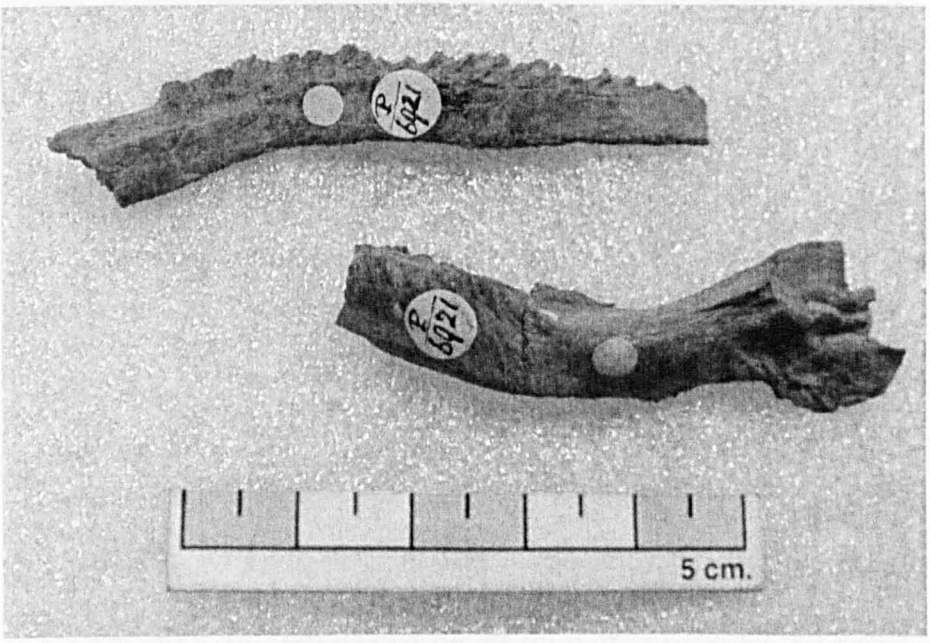


Figure 6.1. The gill raker fragments figured by Arthur Smith Woodward in 1890, in lateral view. Scale = 50mm.

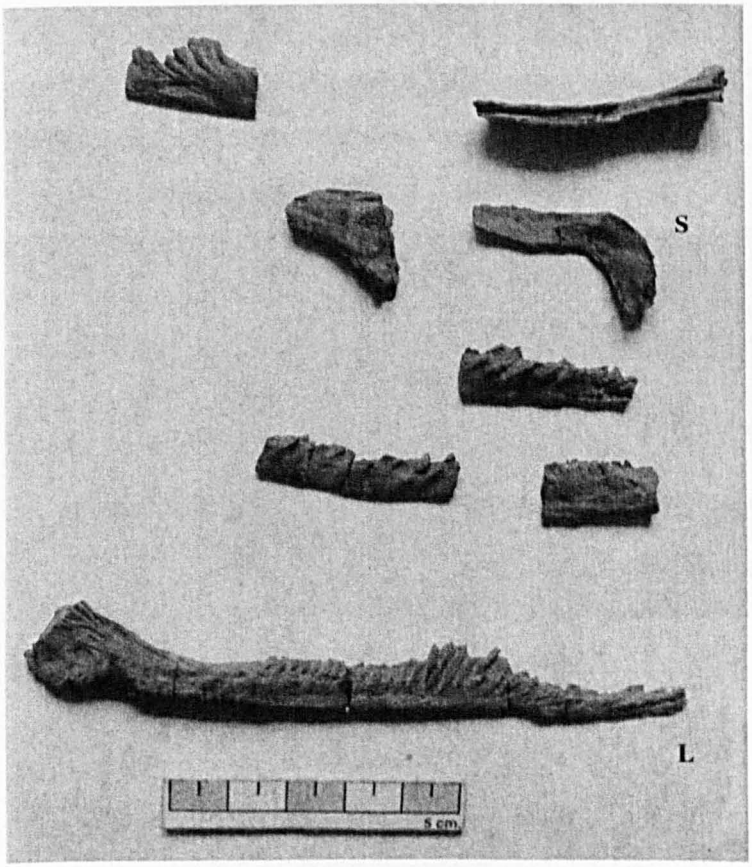


Figure 6.2. Other gill raker elements, including the two complete gill rakers, in lateral view. 112mm gill raker = L, 39mm gill raker = S. Scale = 50mm.

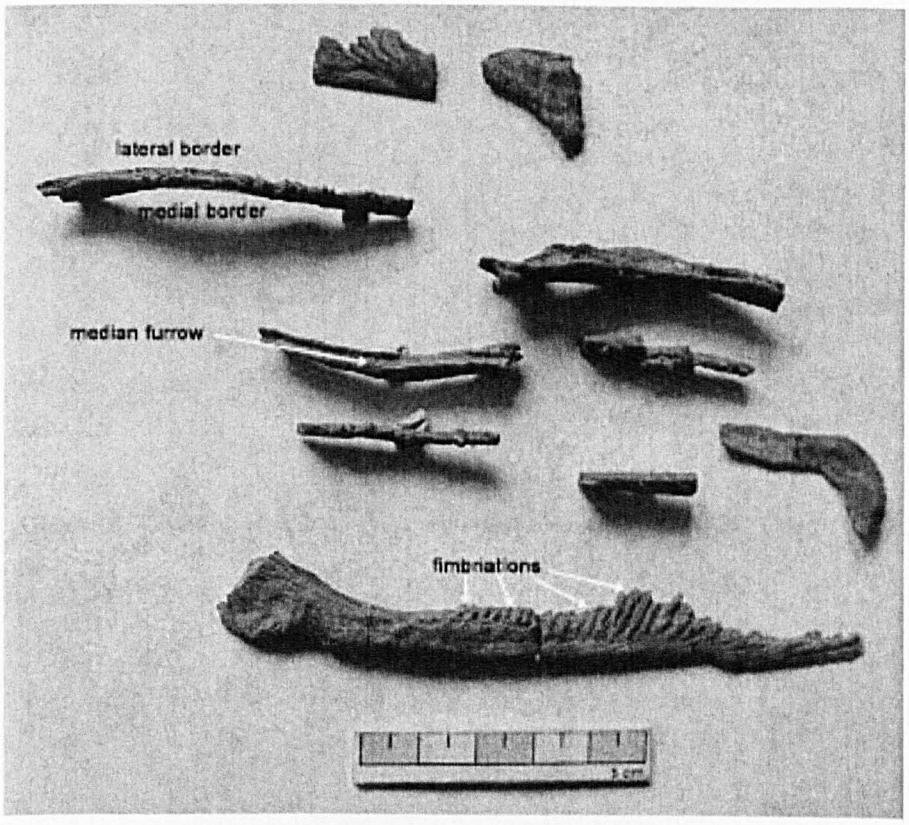


Figure 6.3. Plan views of gill raker fragments. Scale = 50mm.

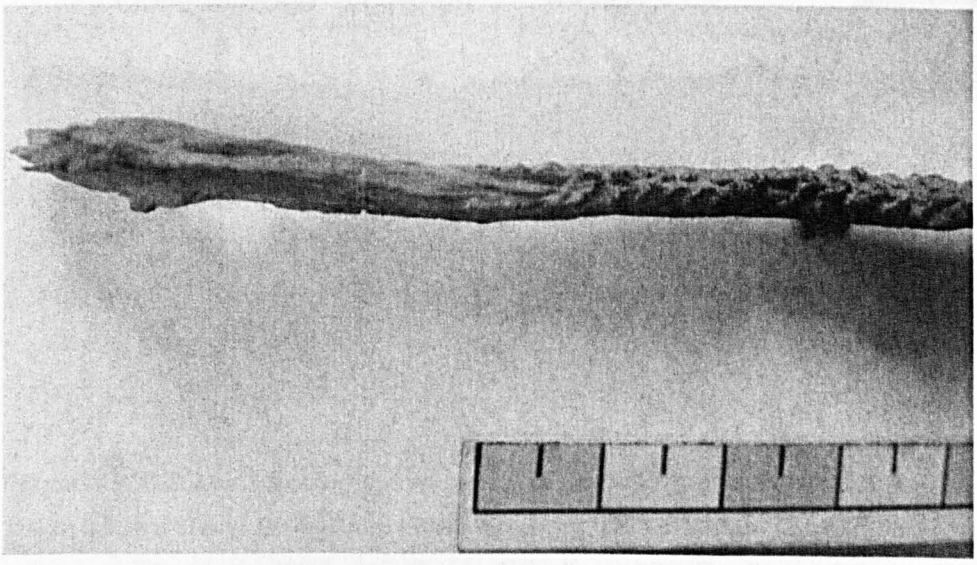


Figure 6.4. Plan view of longest gill raker. Scale = 50mm.

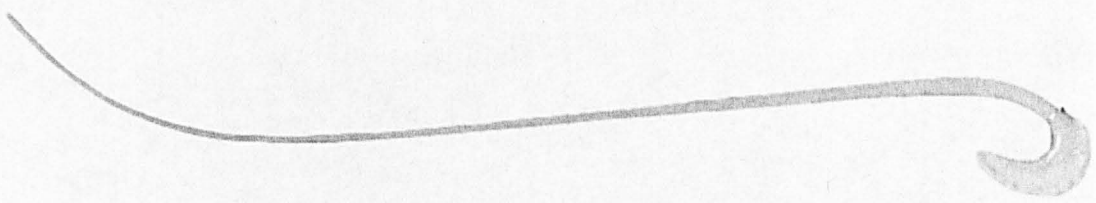


Figure 6.5. Gill raker of basking shark, *Cetorhinus maximus* (GLAHM 130511). Gill raker = 104mm long.

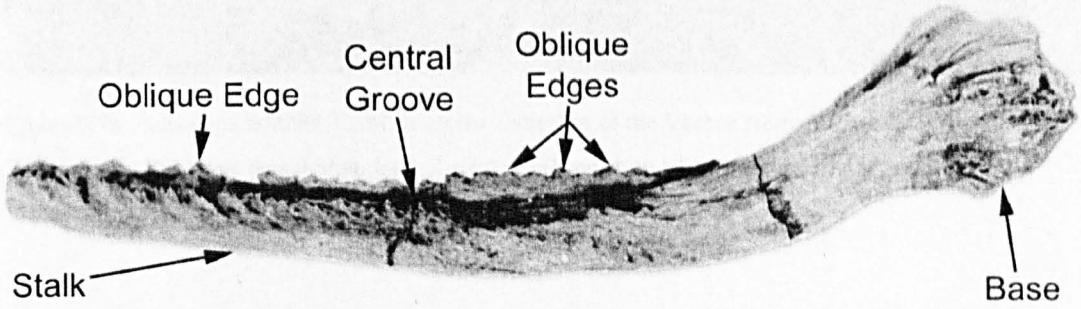


Figure 6.6. Gill raker of *Leedsichthys problematicus* (BMNH P.8610), to show main features of a gill raker, length = 81mm. Oblique edge (Smith Woodward 1889) = 'process' (Yasuda 1960) = 'lateral plications' (Martill *et al.* 1999); stalk (Peirong 1989; Kazanski 1964) = Ramus (Martill *et al.* 1999); base (Peirong 1989), the site of insertion of raker abducting muscle (*Interbranchiales abductores*, Winterbottom 1974; *Abductor branchiospinalis*, van den Berg *et al.* 1994). Photograph after Martill.

Figure 6.7a. Specimen BMNH 32581, from the Callovian of the Vaches Noire, included in Woodward's 1889 type description. Lateral view of gill raker, width of block in field of view = 129mm.

Figure 6.7b. Specimen BMNH 32581, from the Callovian of the Vaches Noire, included in Woodward's 1889 type description. Lateral view of gill raker on edge of block, length of gill raker fragment = 51mm.

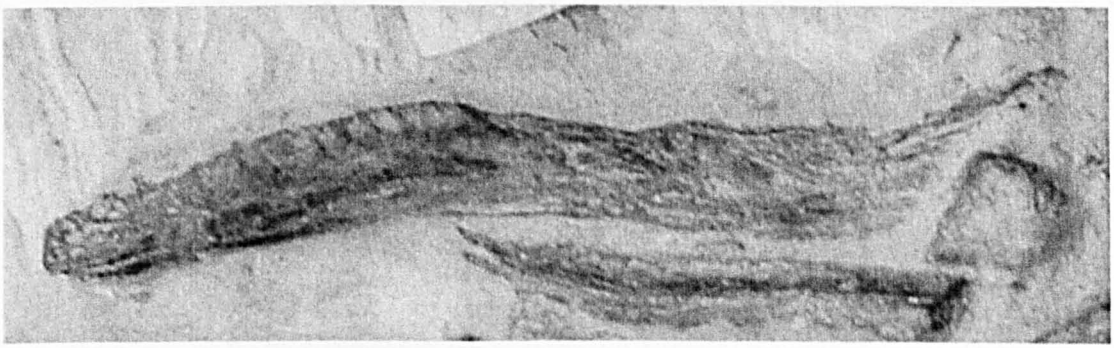


Figure 6.7c. Specimen BMNH 32581, from the Callovian of the Vaches Noire, included in Woodward's 1889 type description. View of gill raker with flanged edge on inferior surface of block, length of gill raker = 61mm.

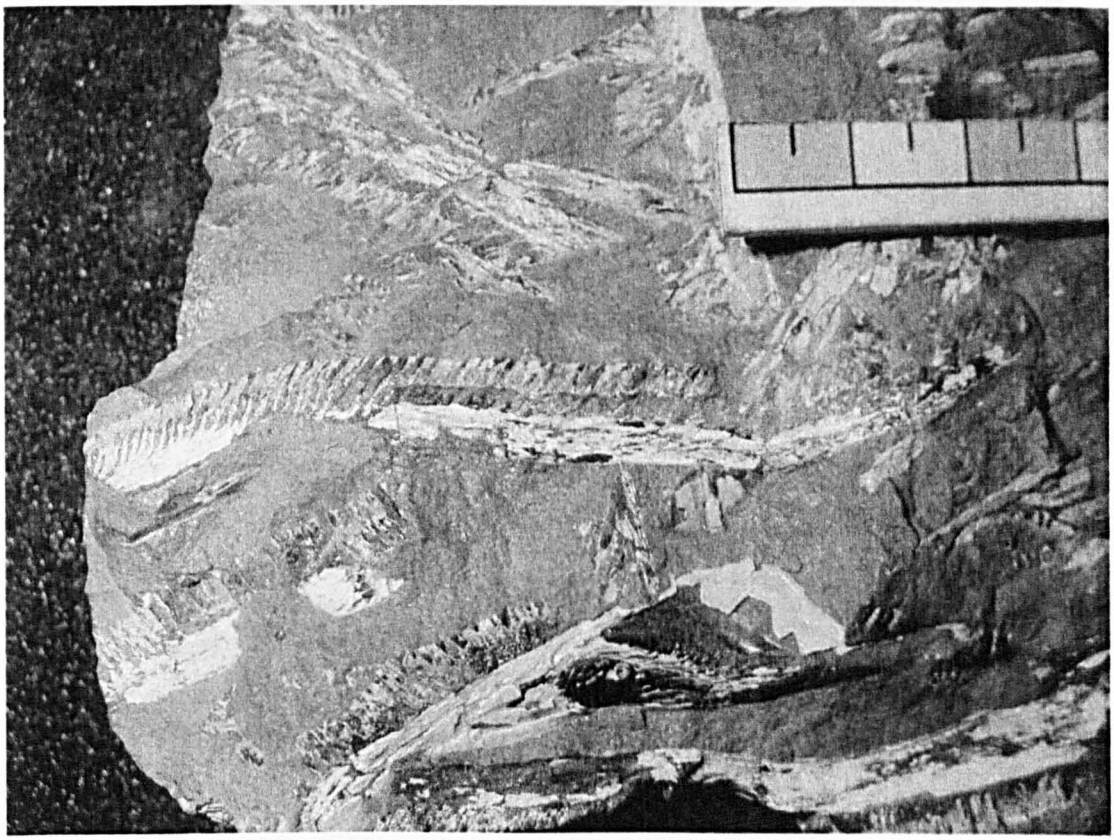


Figure 6.8. Detail of SMNK 2573.PAL, the holotype specimen of *Leedsichthys notocetes*.
Field of view = 103mm.

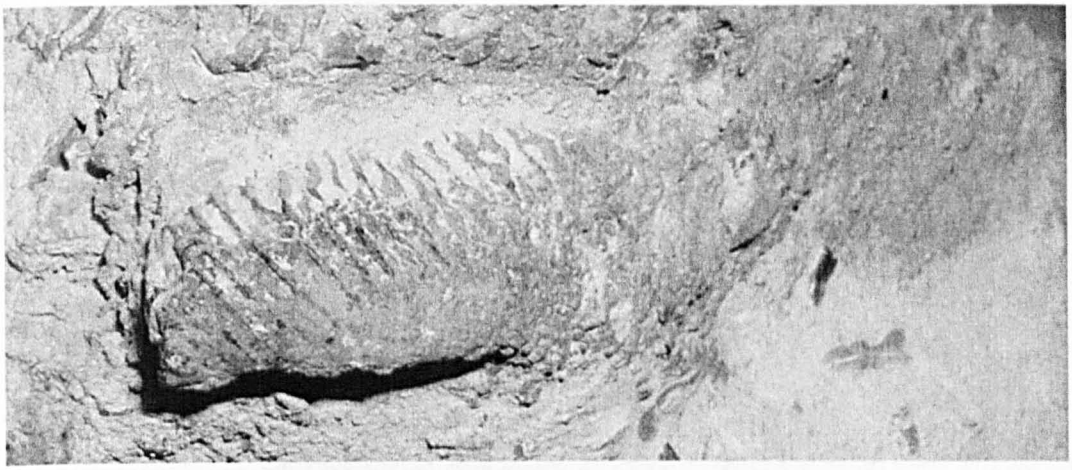


Figure 6.9a. Gill raker from Callovian of Normandie (length around 70mm, Collection Pennettier). Detail from distal end, showing oblique edges.

Figure 6.9b. Gill raker from Callovian of Normandie (length around 70mm, Collection Pennettier). Lateral view showing oblique edges forming transverse planes across the gill raker.

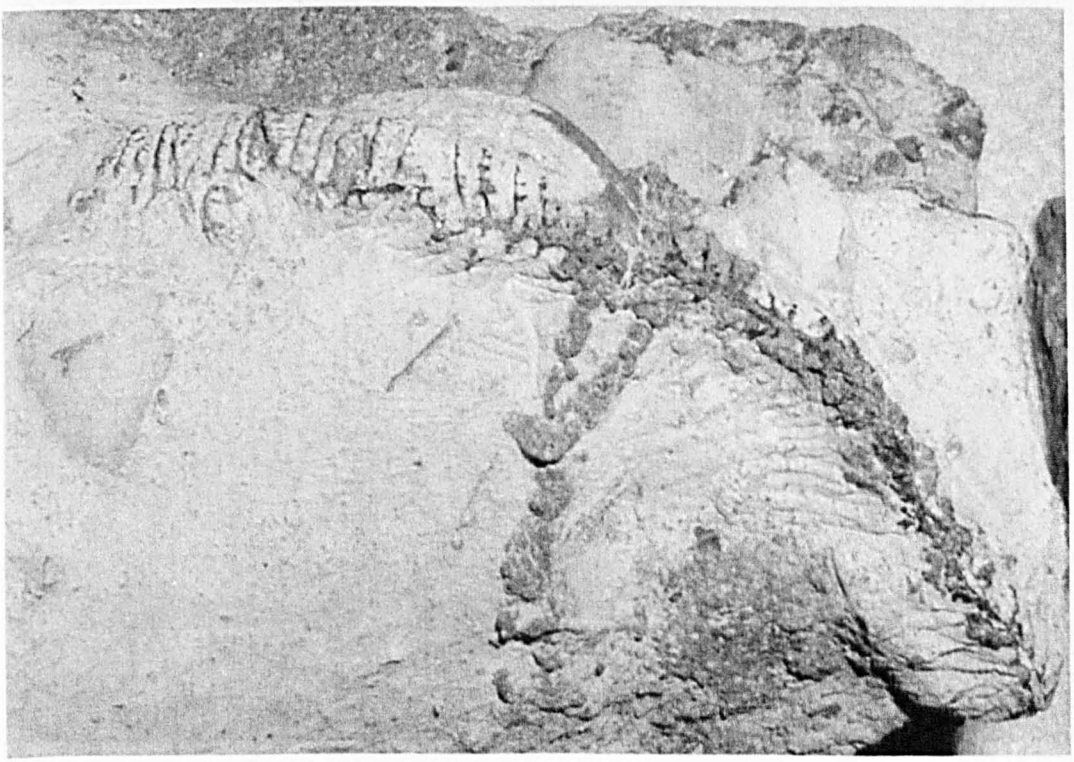


Figure 6.9c. Gill raker from Callovian of Normandie (length around 70mm, Collection Pennettier). Plan view of gill raker, showing median septum.

Figure 6.10. Gill raker (G.1073J) from Upper Kimmeridgian of Cap de la Heve. Length = 83mm, photograph courtesy of D. Gielen.

Figure 6.11. Specimen I19-1 21 73, disarticulated gill rakers, collected from Antofagasta in January 1973. Scale = 100mm.

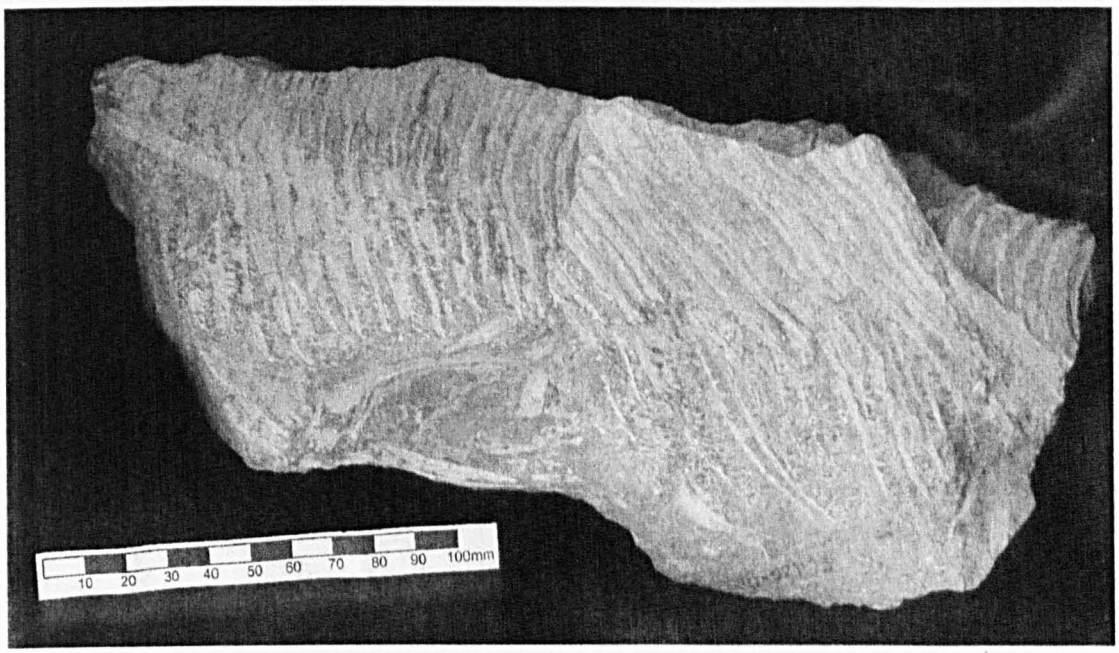


Figure 6.12. Specimen I8-02 11 73, articulated gill rakers, collected from Antofagasta in February 1973. Scale = 100mm.

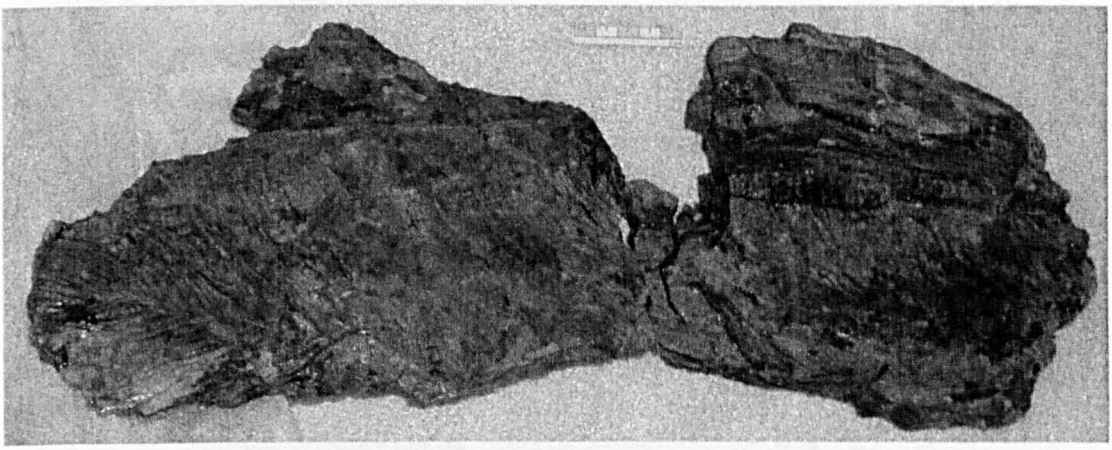


Figure 6.13a. PETMG F34, gill basket with cranial elements. Dorsal view of specimen. Scale = 50mm.

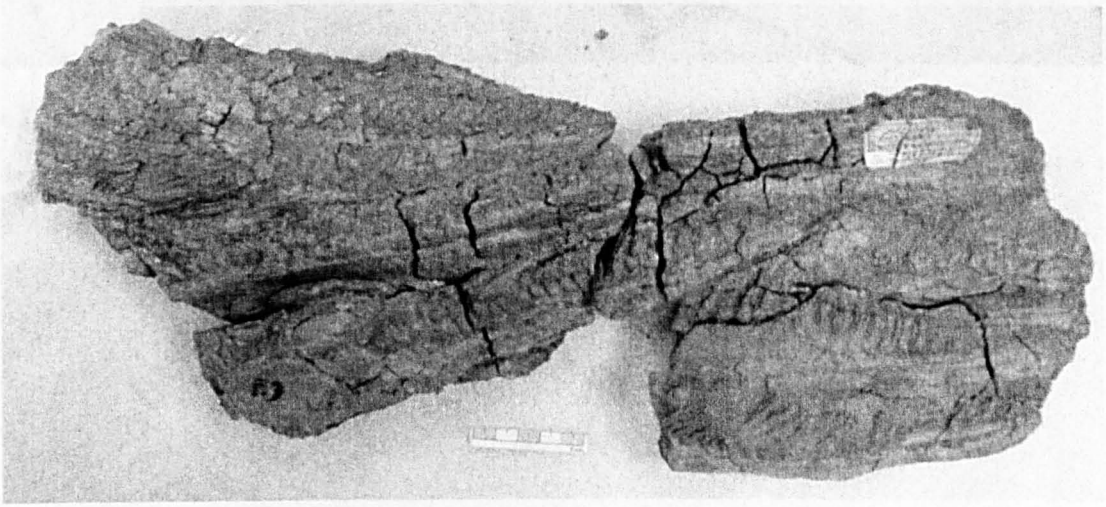


Figure 6.13b. PETMG F34, gill basket with cranial elements. Ventral view of specimen. Scale = 50mm.

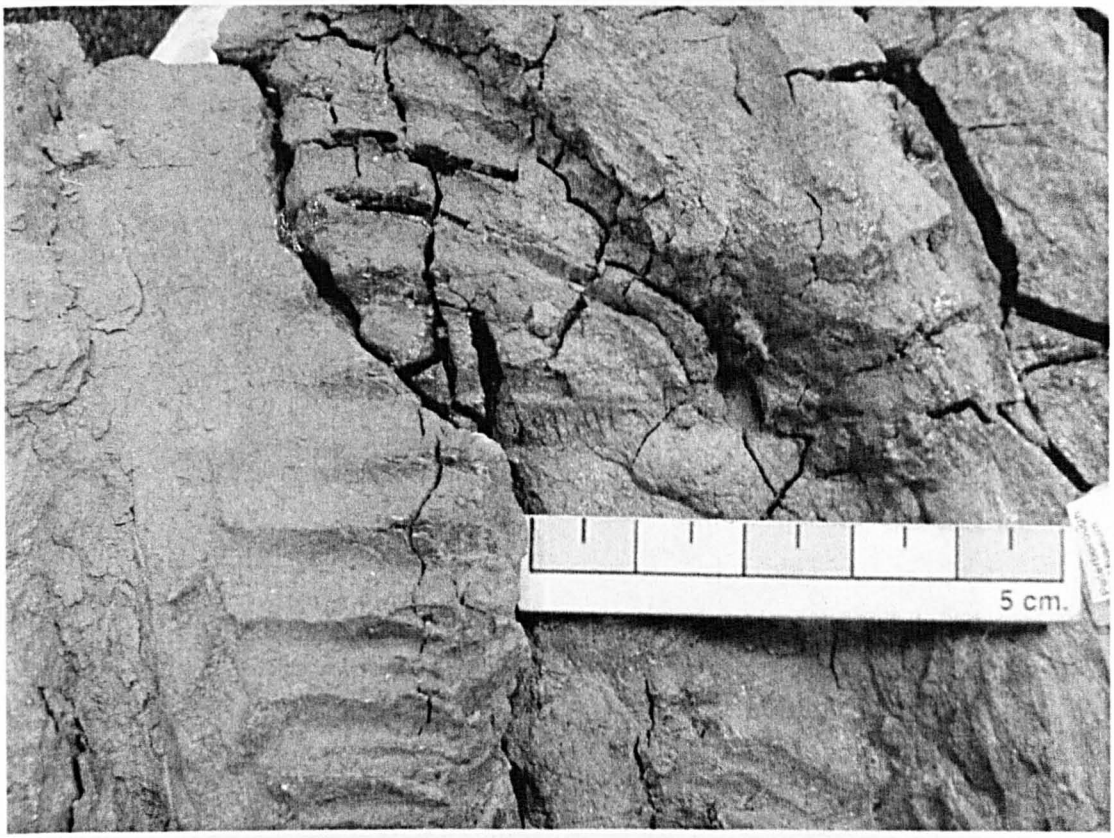


Figure 6.14. PETMG F34, gill basket with cranial elements. Detail of ventral surface, showing gill rakers with *acus fanunculorum*. Scale = 50mm.

Figure 6.15. PETMG F34, gill basket with cranial elements. Detail of fragment from PETMG F34, coated in ammonium chloride. Edge = E, Socket = S. Field of view = 17mm wide. Photograph courtesy of D. M. Martill.

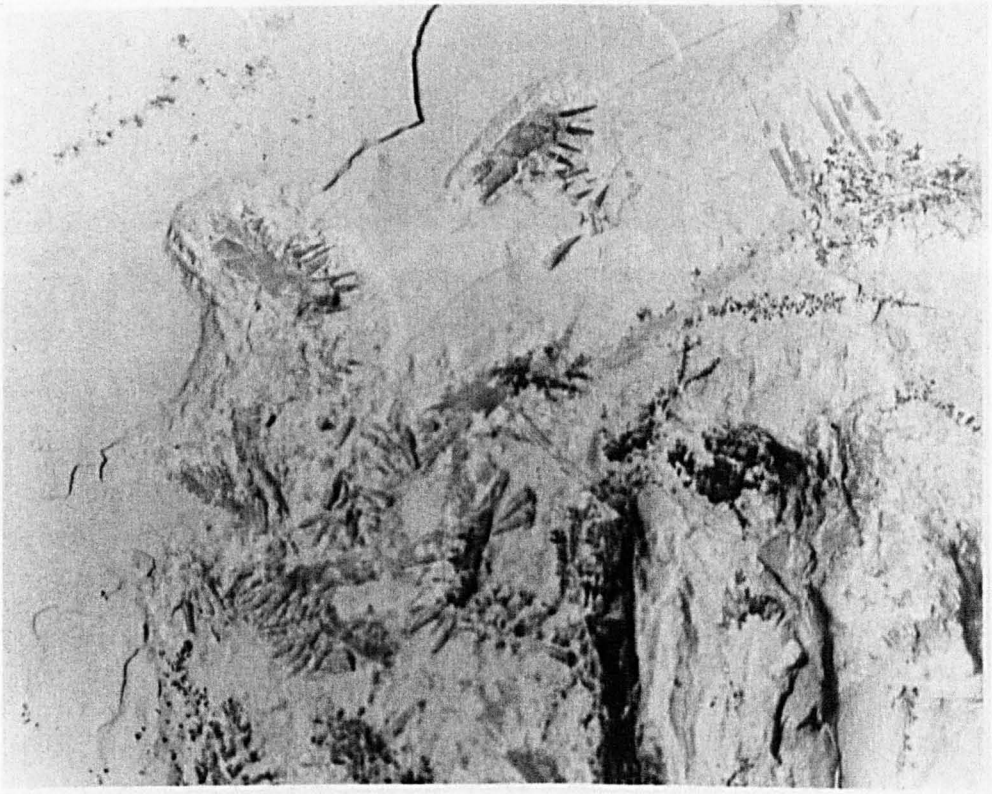


Figure 6.16. Detail from Leich Collection specimen L.1309. Putative gill rakers of *Asthenocormus*. Original photograph courtesy of Lambers, no scale recorded.

Figure 6.17. SMNK 2573.PAL, the holotype specimen of *Leedsichthys notocetes*. Legend – r1-7 = gill raker fragments 1-7, m = fragments of 'mesh'. Block is 142mm long and 67mm high.

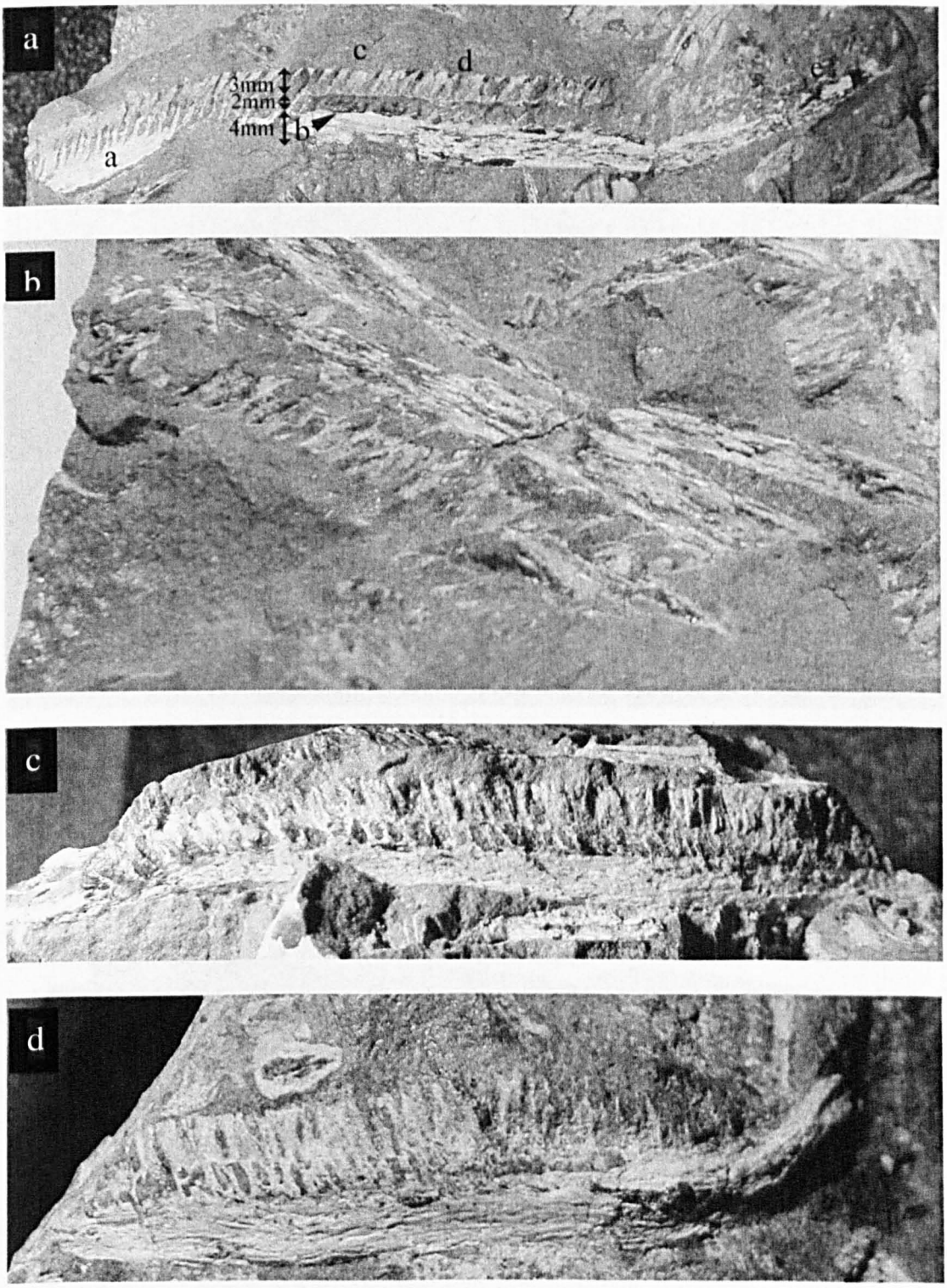


Figure 6.18a, b, c, d from top: SMNK 2573.PAL, the holotype specimen of *Leedsichthys notocetes*.
a - Gill raker fragment 1 (r1), field of view = 90mm. For legend for points a-e, see text.
b - Gill raker fragment 2 (r2), field of view = 15mm.
c - Gill raker fragment 3 (r3), field of view = 75mm.
d - Gill raker fragment 4 (r4), field of view = 60mm.

Figure 6.19a. Ventral fenestrae (V) with lateral fenestrae (L) on block of articulated gill rakers, collected from Antofagasta in February 1973, specimen I8-02 11 73. Field of view = 70mm wide.

Figure 6.19b. Longitudinal section of gill raker from *Leedsichthys problematicus* (specimen 'Ariston', PETMG F174/2052), showing internal gill raker cavity. Length of gill raker = 70mm.

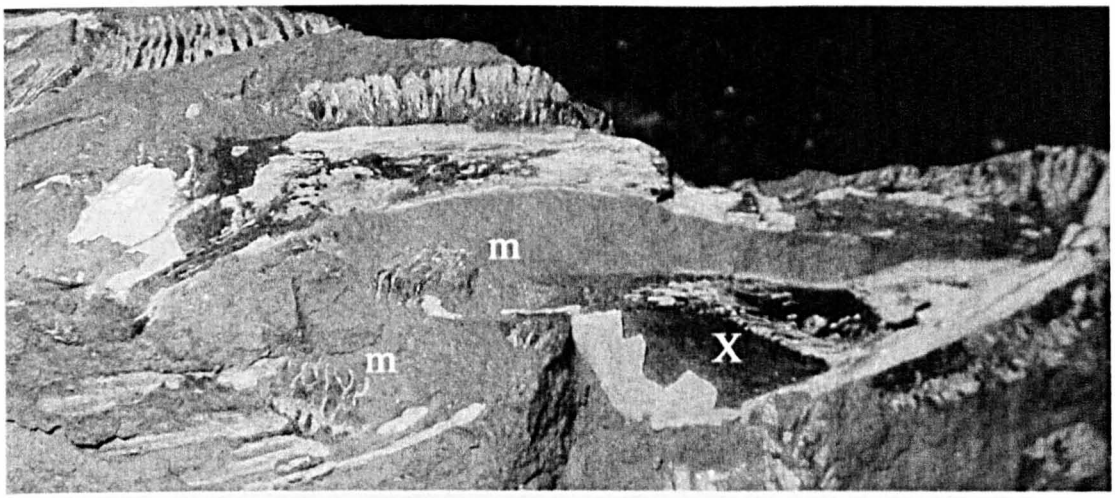


Figure 6.20. SMNK 2573.PAL. Black contact area (X) on gill raker fragment 7 (r7), with nearby fragments of 'mesh' (m). Field of view = 80mm.

Figure 6.21. Detail of SMNK 2573.PAL *Leedsichthys notocetes* block, showing transverse section of gill raker with extensive internal resorption. Field of view = 25mm wide.

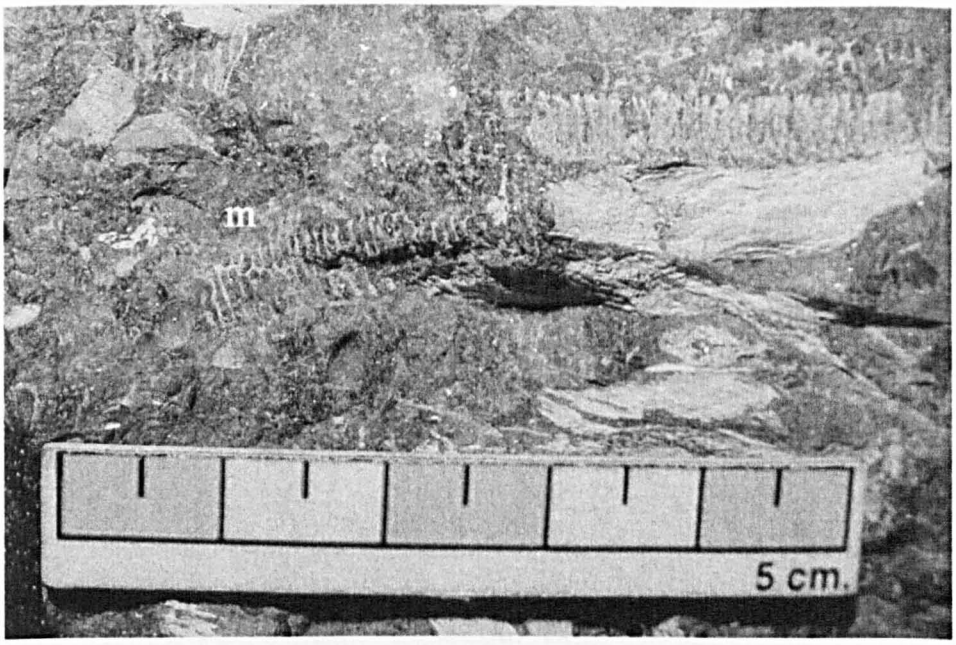


Figure 6.22. Detail of disarticulated gill raker block, collected from Antofagasta in January 1973, specimen I19-1 21 73, showing 'mesh' fragments. Scale = 50mm.

Figure 6.23. Acid-etched fragment from SMNK2573.PAL block with transverse sections through stalks of gill rakers outlined on side of fragment leading up to perpendicular surface and transforming into 'mesh' pattern (after Steel, August 2004). Field of View = 45mm wide.

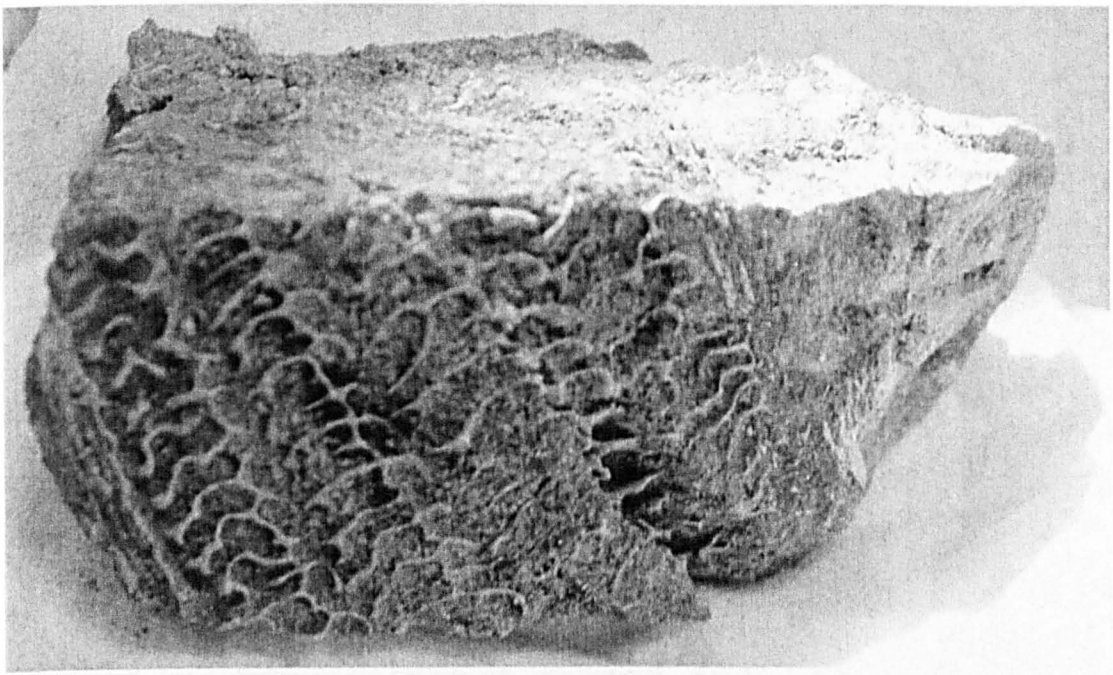


Figure 6.24. Acid-etched fragment from SMNK2573.PAL block, with plan view of fragment, showing 'mesh' etched from surface of limestone matrix, cross-linking from gill raker to gill raker. Fragment = 40mm wide.

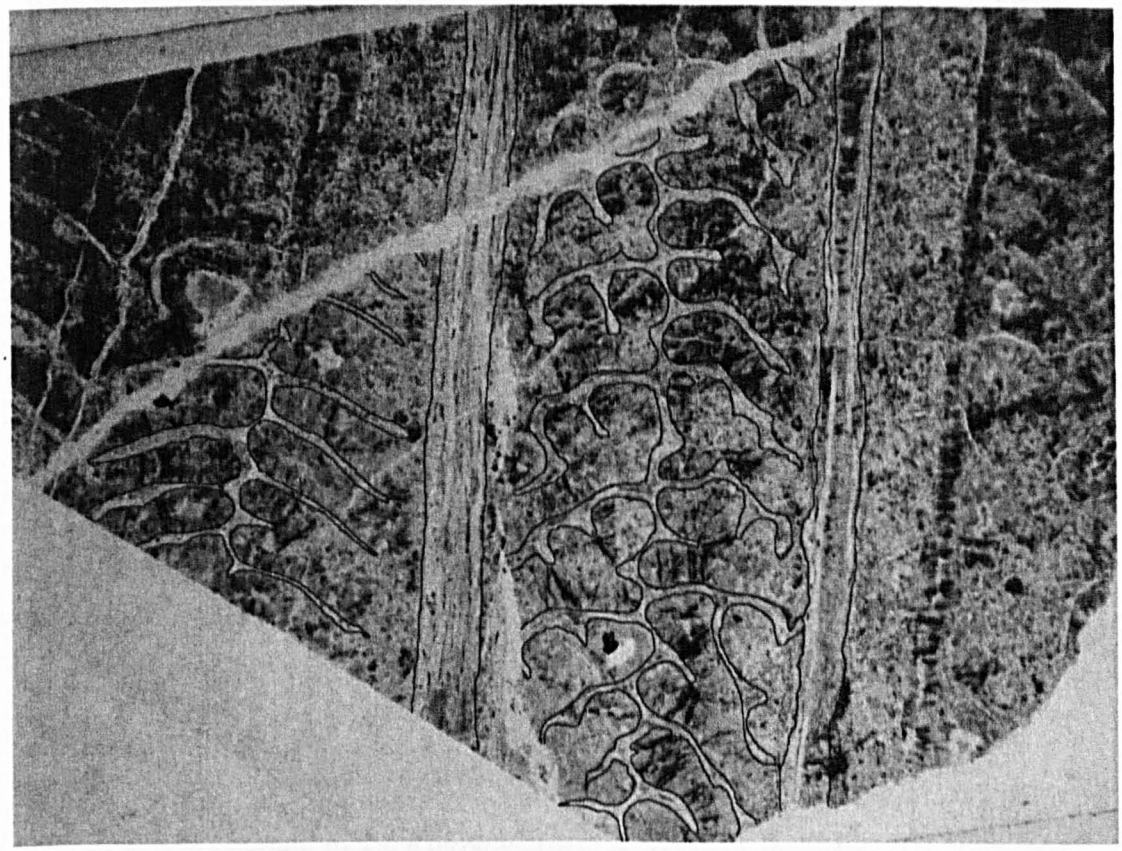


Figure 6.25a. Outline drawing overlying thin-sections of fragment from SMNK 2573.PAL block, from 'plan view perspective'. Interraker gap (distance from centre of gill raker stalk to adjacent centre of gill raker stalk) = 19mm.

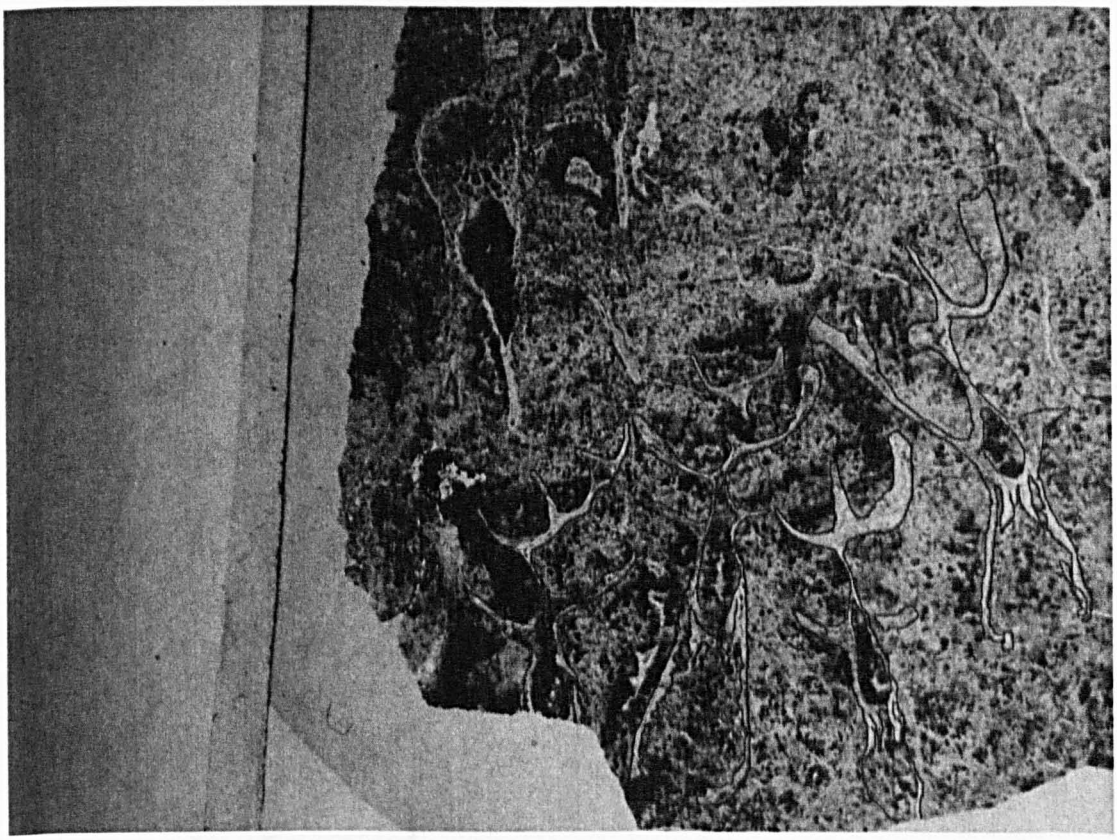


Figure 6.25b. Figure 6.25b Outline drawing overlying transverse thin-section of fragment from SMNK 2573.PAL block. Field of view height = 23mm.

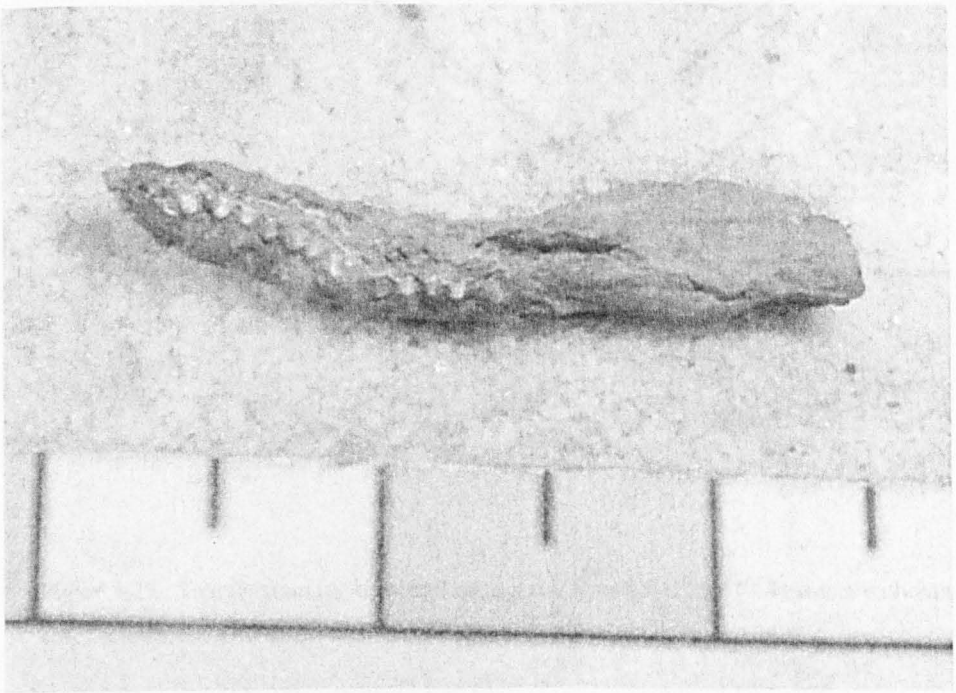


Figure 6.26. Gill raker from BMNH P.10000 displaying anomalous structure inbase of median furrow. Possibility that it could be invertebrate shell fragment aligned with raker by chance, or could be related to mesh structure in median furrow of *Leedsichthys* gill rakers from localities outwith Peterborough district. Scale bar shows 25mm width.

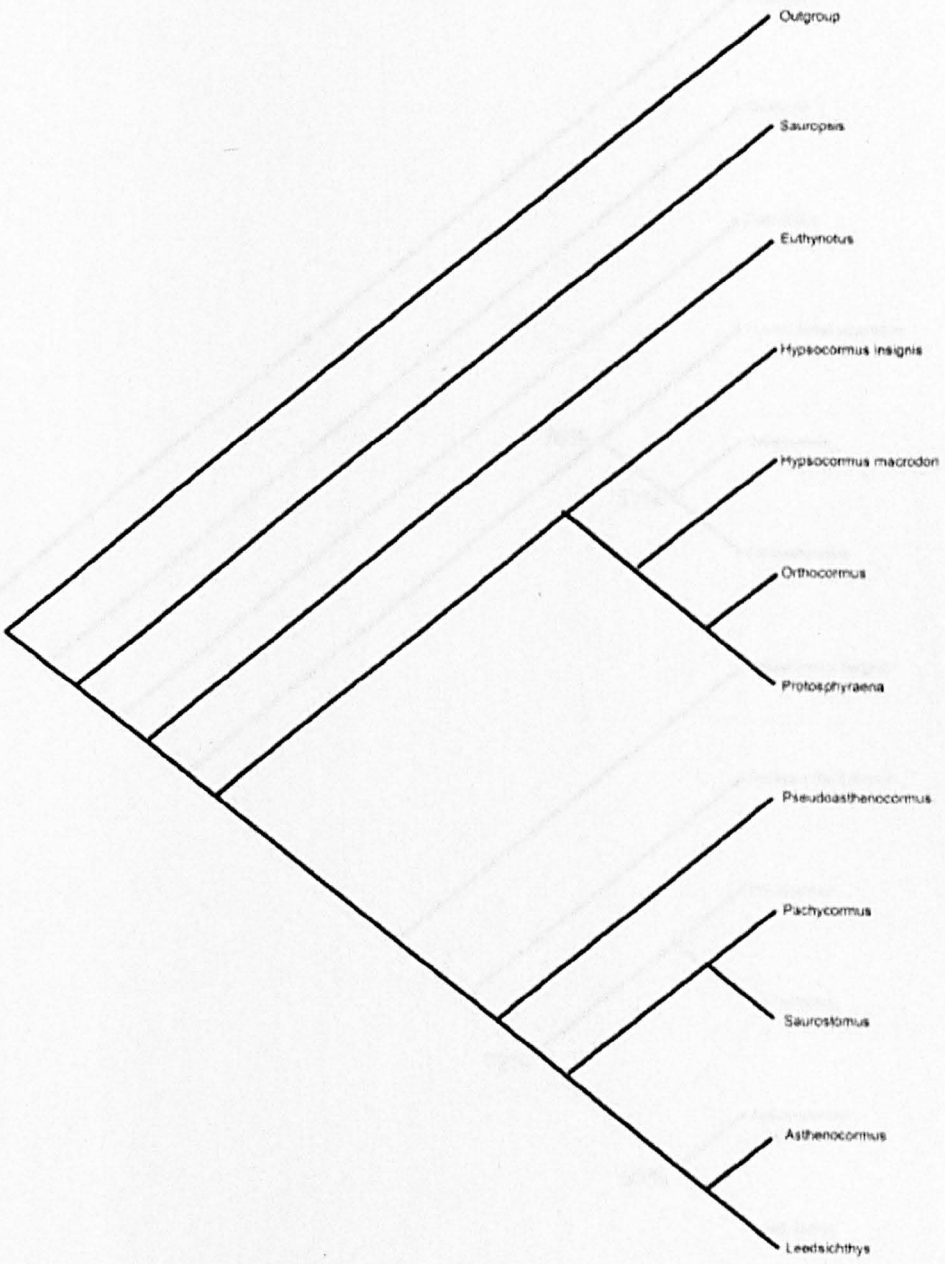


Figure 6.27. Tree diagram for Lambers' dataset run Unordered for 15 characters without 'Taxon 13' - strict consensus of 46 trees (each of 34 steps).

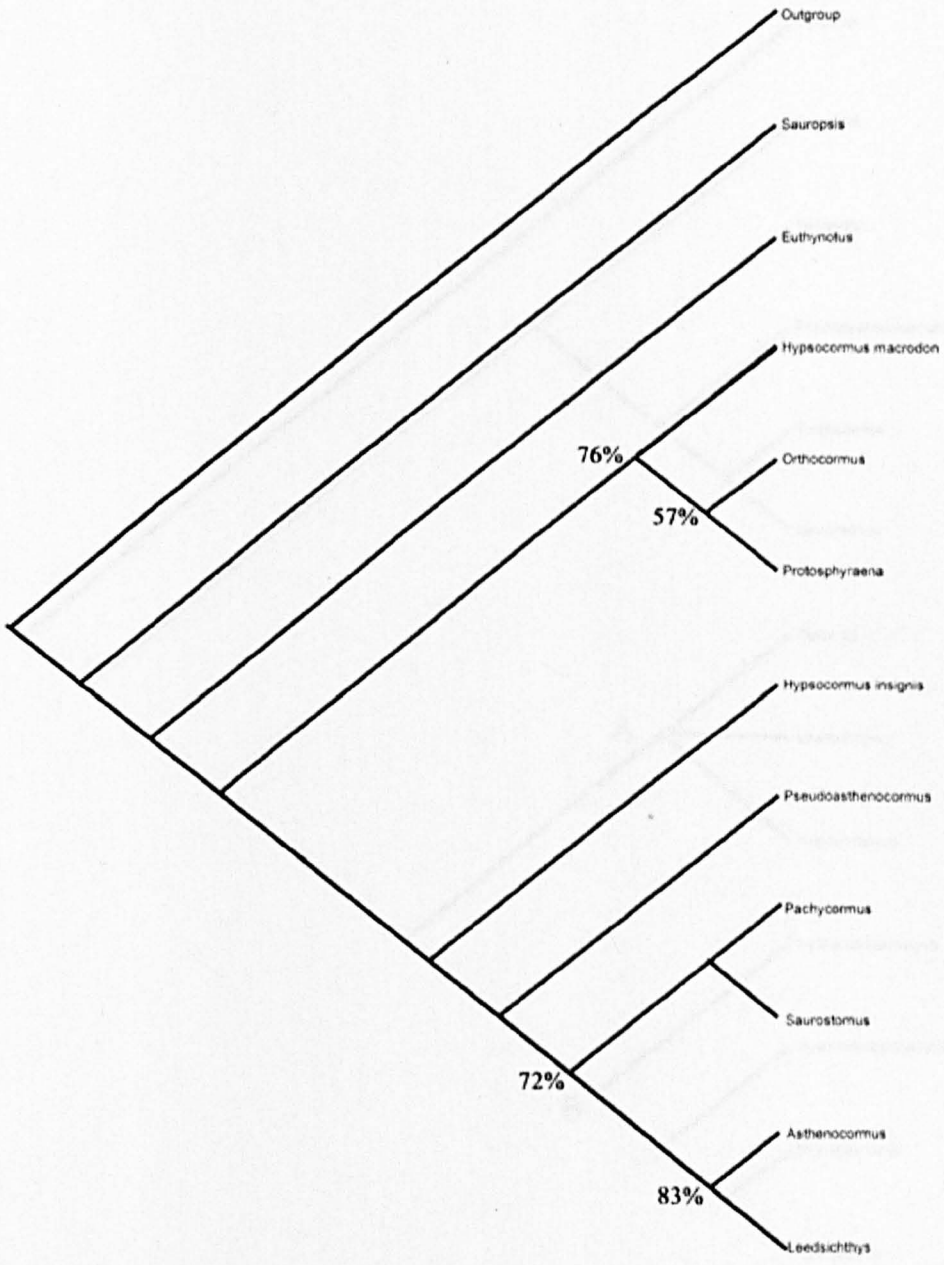


Figure 6.28. Tree diagram for Lambers' dataset run Unordered for 15 characters without 'Taxon 13' - 50% majority rule of 46 trees.

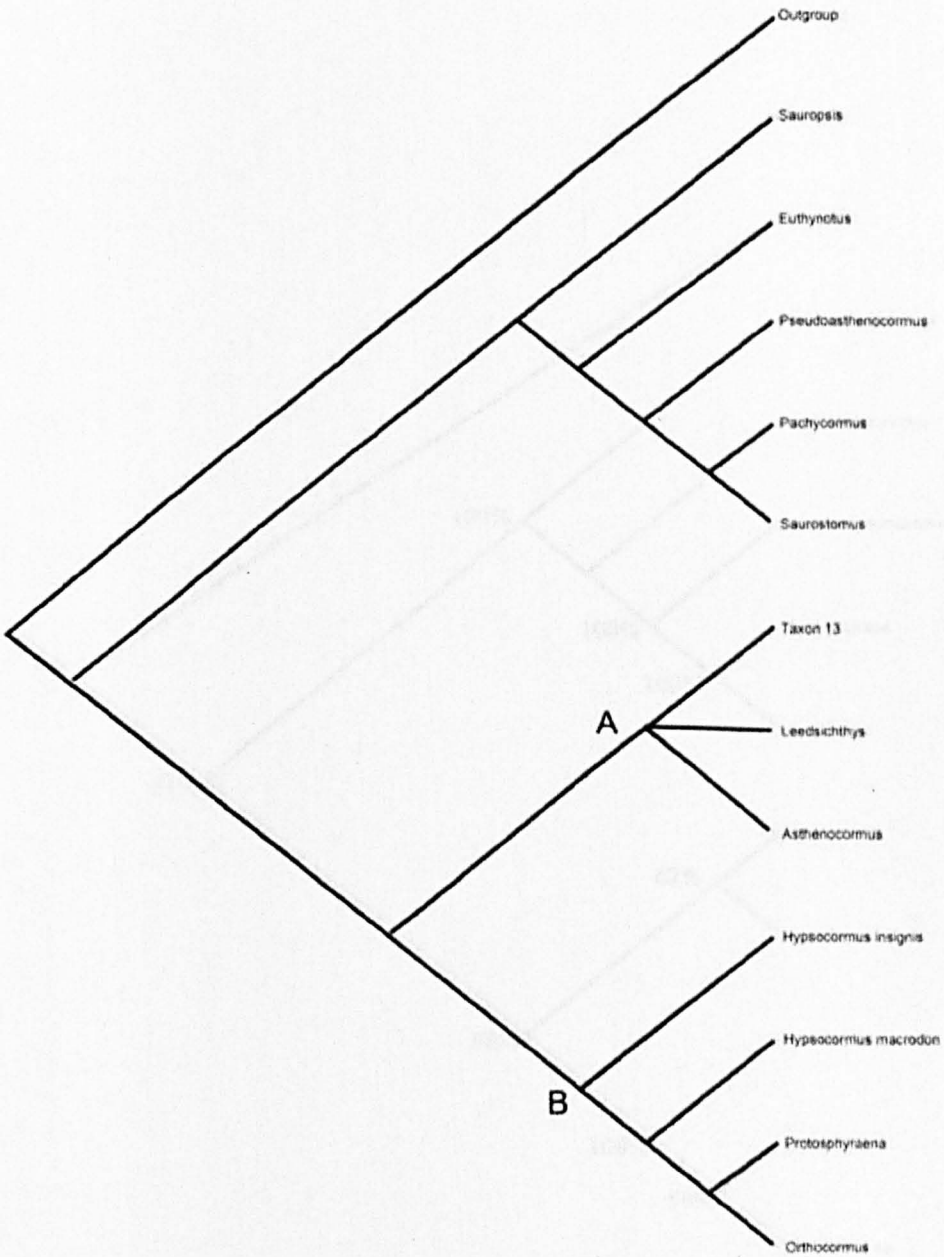


Figure 6.29. Tree diagram for revised and expanded 16 character dataset for 13 taxa after Lambers - strict consensus of 45 trees (each of 41 steps).

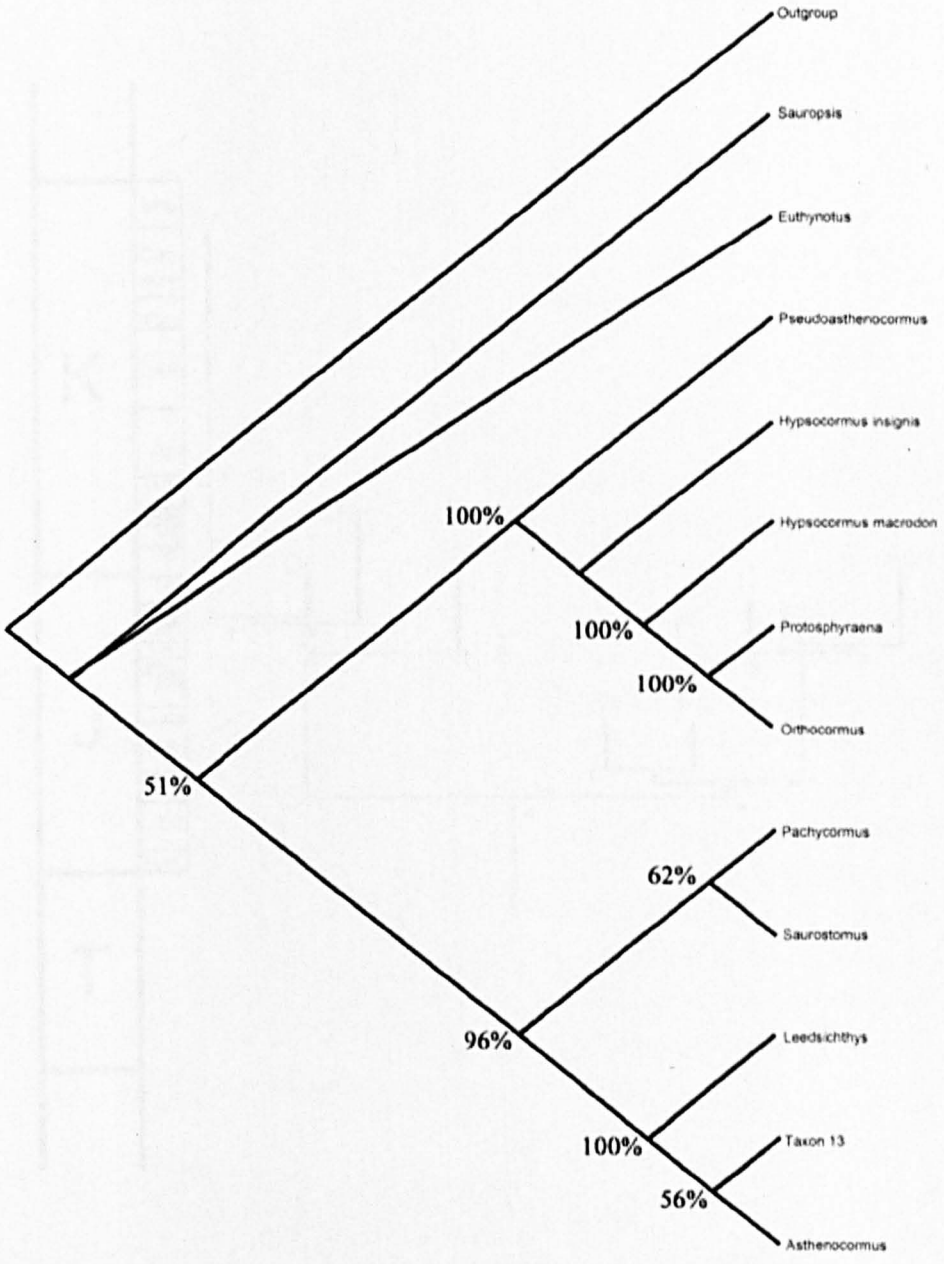


Figure 6.30. Tree diagram for revised and expanded 16 character dataset for 13 taxa after Lambers - 50% majority rule of 45 trees.

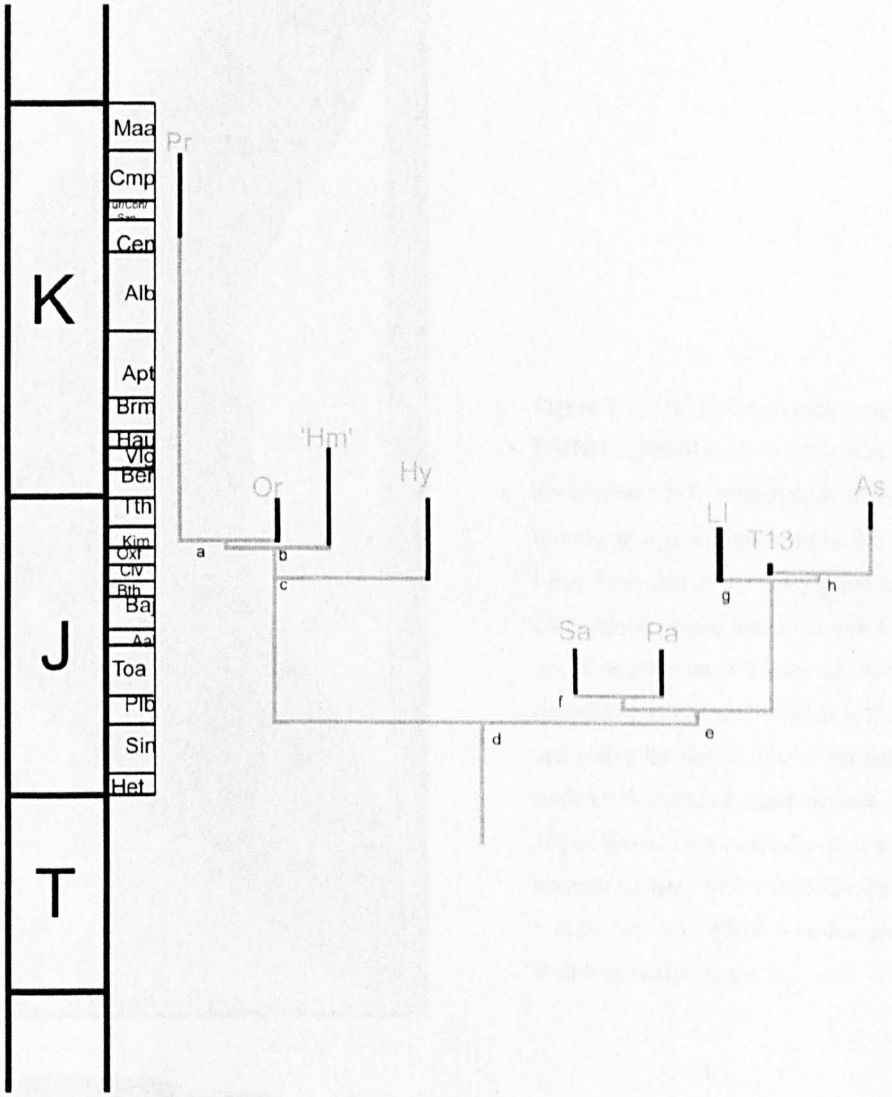


Figure 6.31. Phylogenetic Tree of selected Pachycormiformes in the Mesozoic. Legend: a-h = nodes a-h, Pr = *Protosphyraena*, Or = *Orthocormus*, 'Hm' = '*Hypsocormus macrodon*', Hy = *Hypsocormus insignis* and *leedsi*, Sa = *Saurostomus*, Pa = *Pachycormus*, Ll = *Leedsichthys*, T13 = 'Taxon 13', As = *Asthenocormus*.

Chapter 7: Figures

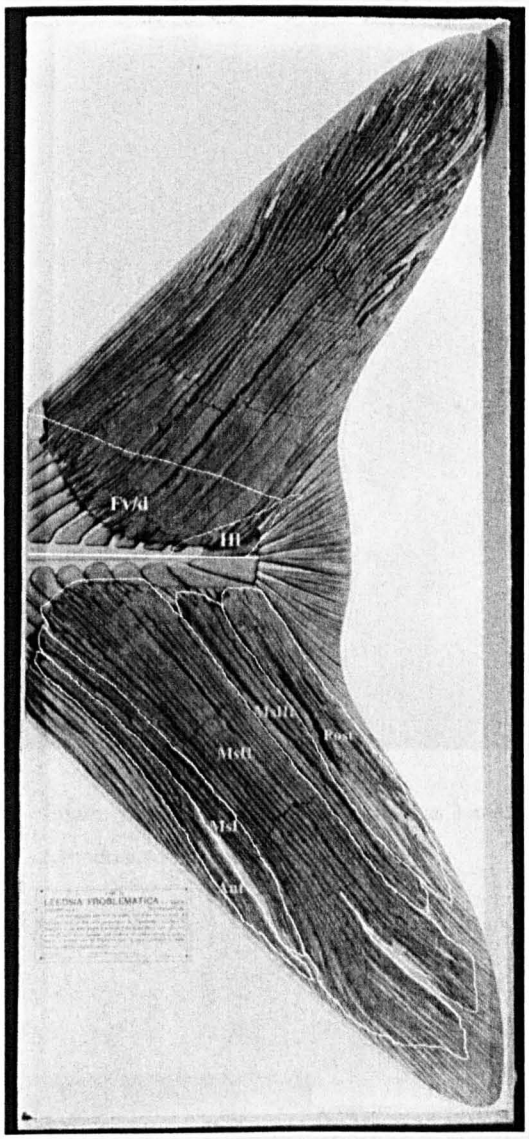


Figure 7.1. The 2740mm high caudal fin of BMNH P.10000 in its display case in September 1937. Attachment areas of muscle groups are indicated on the upper lobe, the extent of the descriptive structural components on the lower. Legend: Fv/d = site of attachment of *Flexor ventralis* or *dorsalis* (it is unknown which is the ventral and which the dorsal lobe of the animal) muscle; HI = site of attachment of *Hypochordal longitudinalis* muscle; Ant = anterior section; MsI = mid-section I; MsII = mid-section II; MsIII = mid-section III; Post = posterior section.

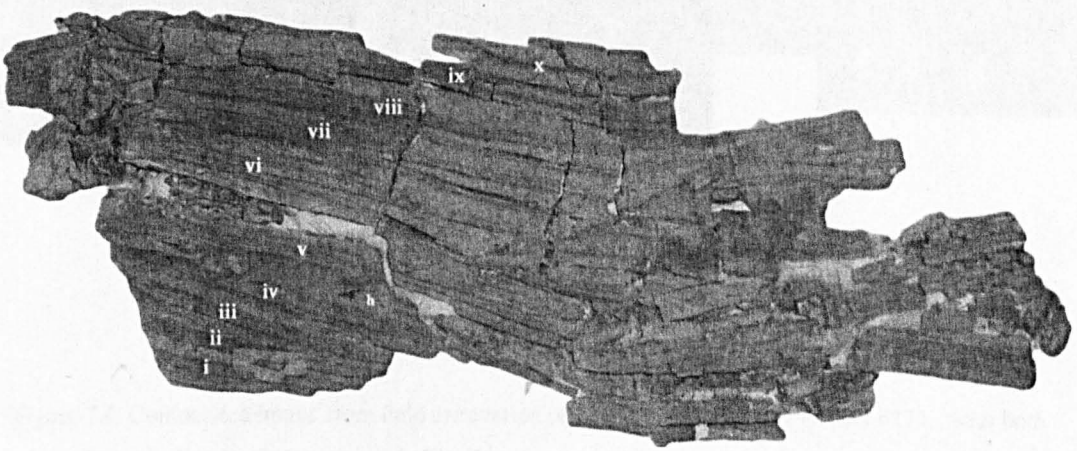


Figure 7.2. The 750mm long fragment of a pectoral fin of BMNH P.10000, before conservation by Melissa Gunter. Proximal end of fin to left of image, leading edge of fin to bottom of image. Legend: i-x = rays 1-10 in text; h = location of hybodont tooth.

Figure 7.3. Detail of area between areas 3 and 6 in Fig. 7.2, near base of overlying ray, showing hybodont tooth (tooth is 17mm wide).

Figure 7.4. Composited image from field excavation of 'Ariston' specimen (PETMG F174), with both pectoral fins outlined, prior to retrieval. The fins are separated from each other by 1005mm of clay. Length of right pectoral fin (RP) = 1363mm. LP = left pectoral fin. Photographs taken by (and used courtesy of) DM Martill on 27/7/2002 in the Star Pit, Whittlesey. Images composited by the author.

Figure 7.5. Ventral aspect of the 1545mm long and 1140 mm wide gill basket of BMNH P.10156 on show in its display case with 870mm long hyomandibula on 9/11/1924, taken by Errol Ivor White. Legend: Cb = ceratobranchial; Ch = ceratohyal; GRs = block of gill rakers; Hb = hypobranchial II; Hh = hypohyal; Hm = hyomandibula; V = fused fifth arch.

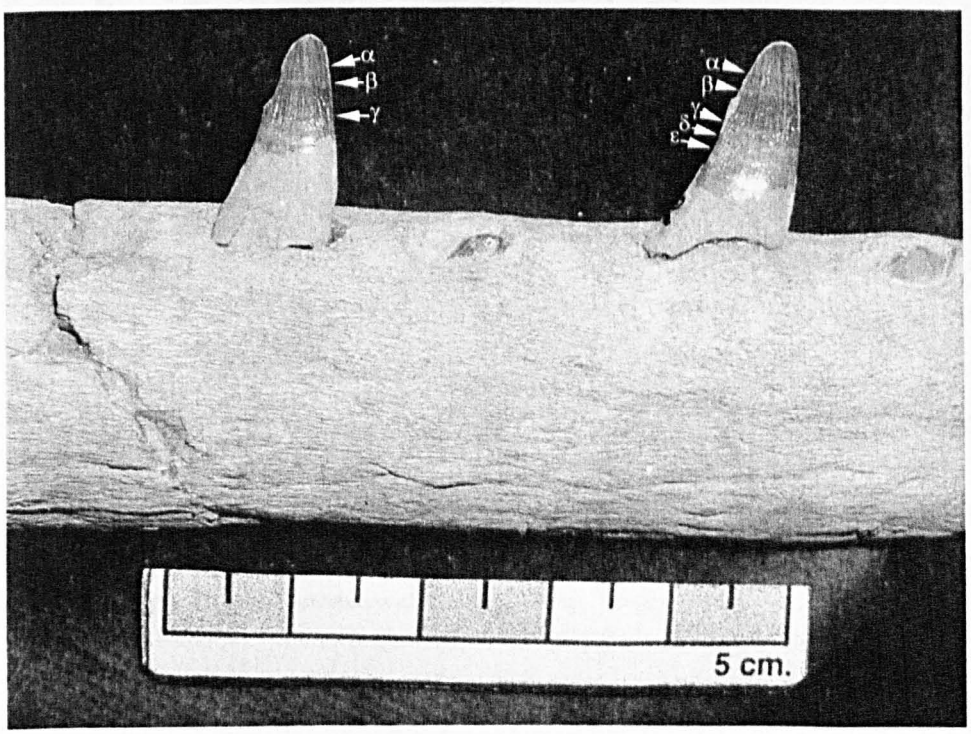


Figure 7.6. The presence of marks of skeletal growth in the teeth of an Oxford Clay metriorhynchid. Comparison of two teeth in the dentary of GLAHM V942, *Metriorhynchus superciliosus*, with correlatable growth lines indicated with Greek lettering. Scale = 50mm.

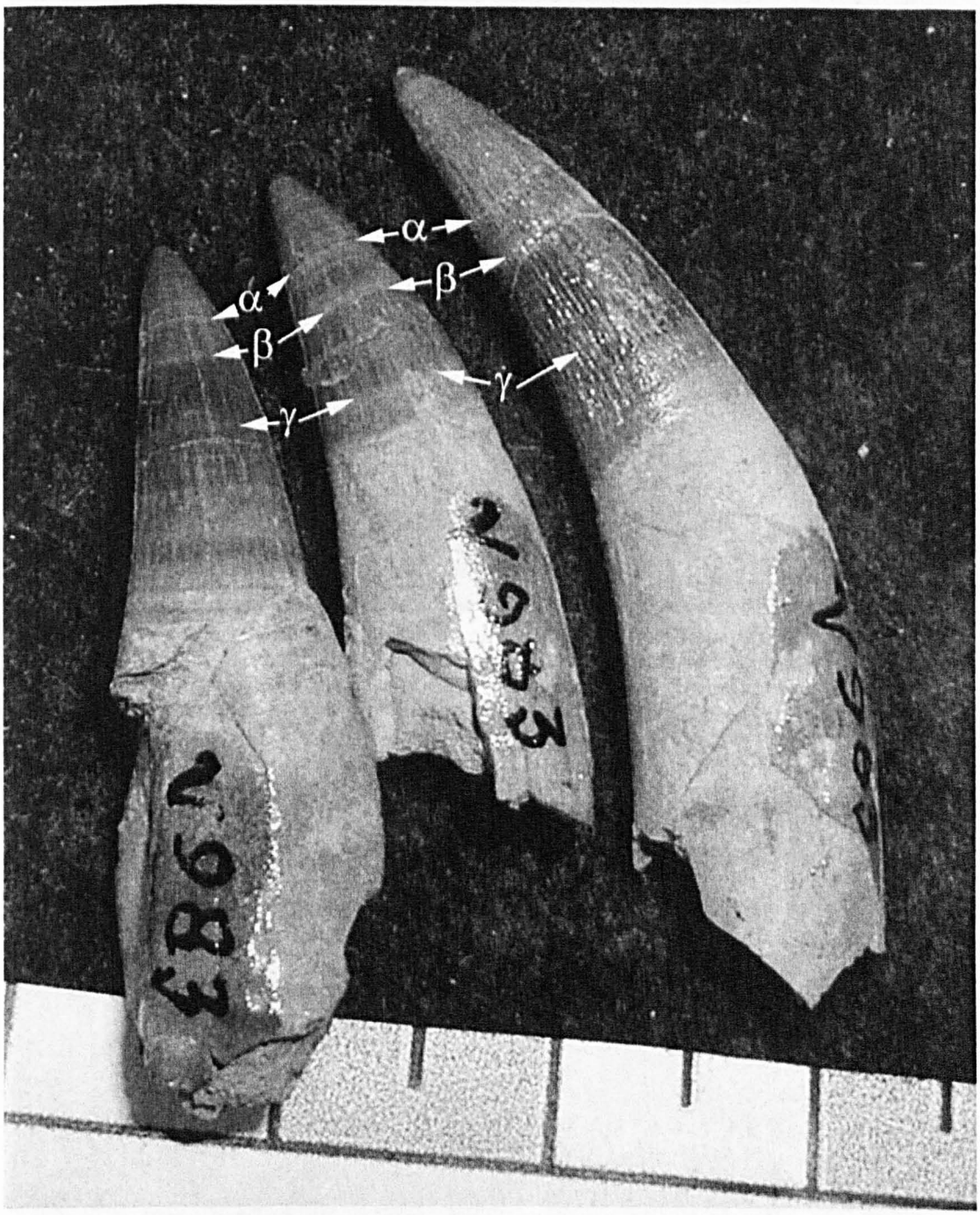


Figure 7.7. The presence of marks of skeletal growth in the teeth of an Oxford Clay metriorhynchid. Comparison of three teeth from specimen GLAHM V983, *Metriorhynchus superciliosus*, with correlatable growth lines indicated with Greek lettering. Scale = 50mm.

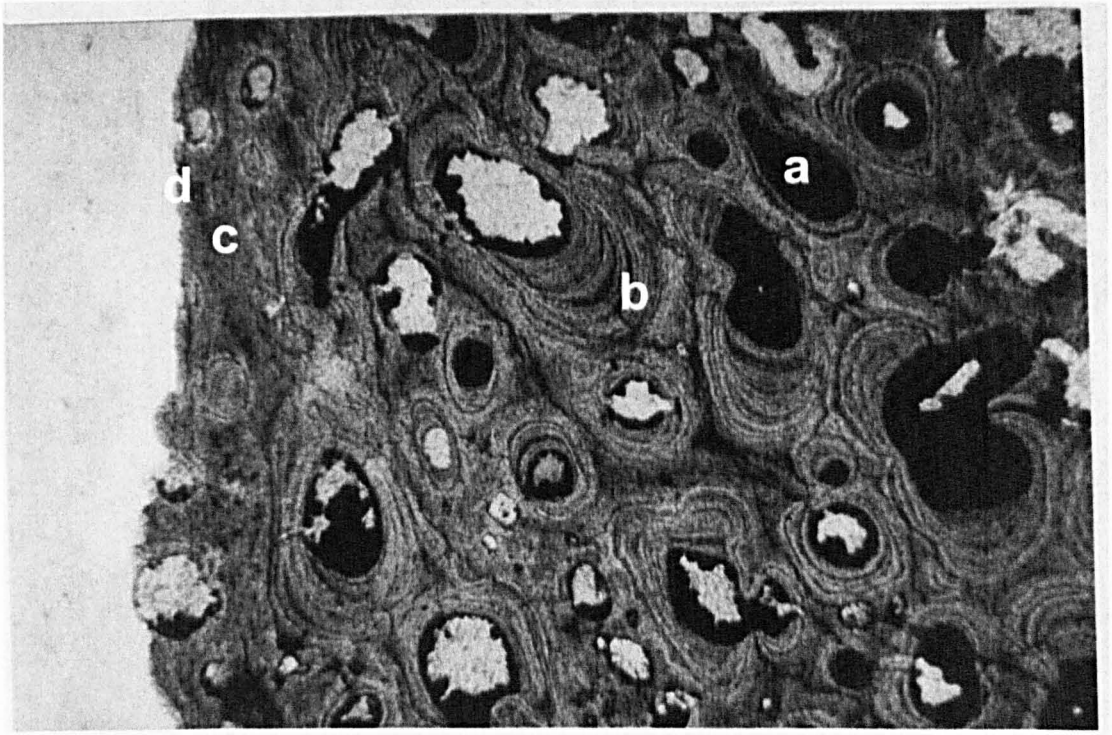


Figure 7.8a. Thin-sections cut and photographed by Martin Büchner from fragments of the Wallücke *Leedsichthys* in 1983, showing compact bone. Legend: a = canal infilled with sediment; b = reticular channel blocked by remodelling; c = relics of primary bone; d = surface of bone showing signs of superficial resorption. Field-of-view is estimated at 2mm wide.

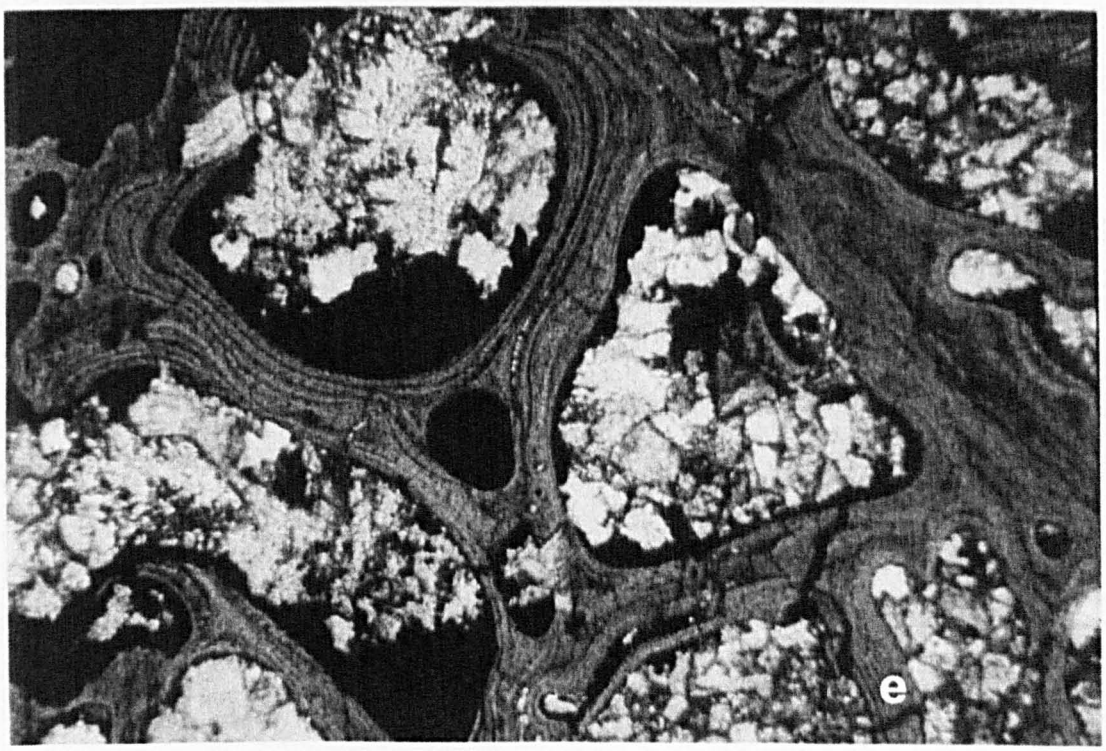


Figure 7.8b. Thin-sections cut and photographed by Martin Büchner from fragments of the Wallücke *Leedsichthys* in 1983, showing detail of cancellous bone. Legend: e = unblocked reticular channel. Field-of-view is estimated at 1mm wide.

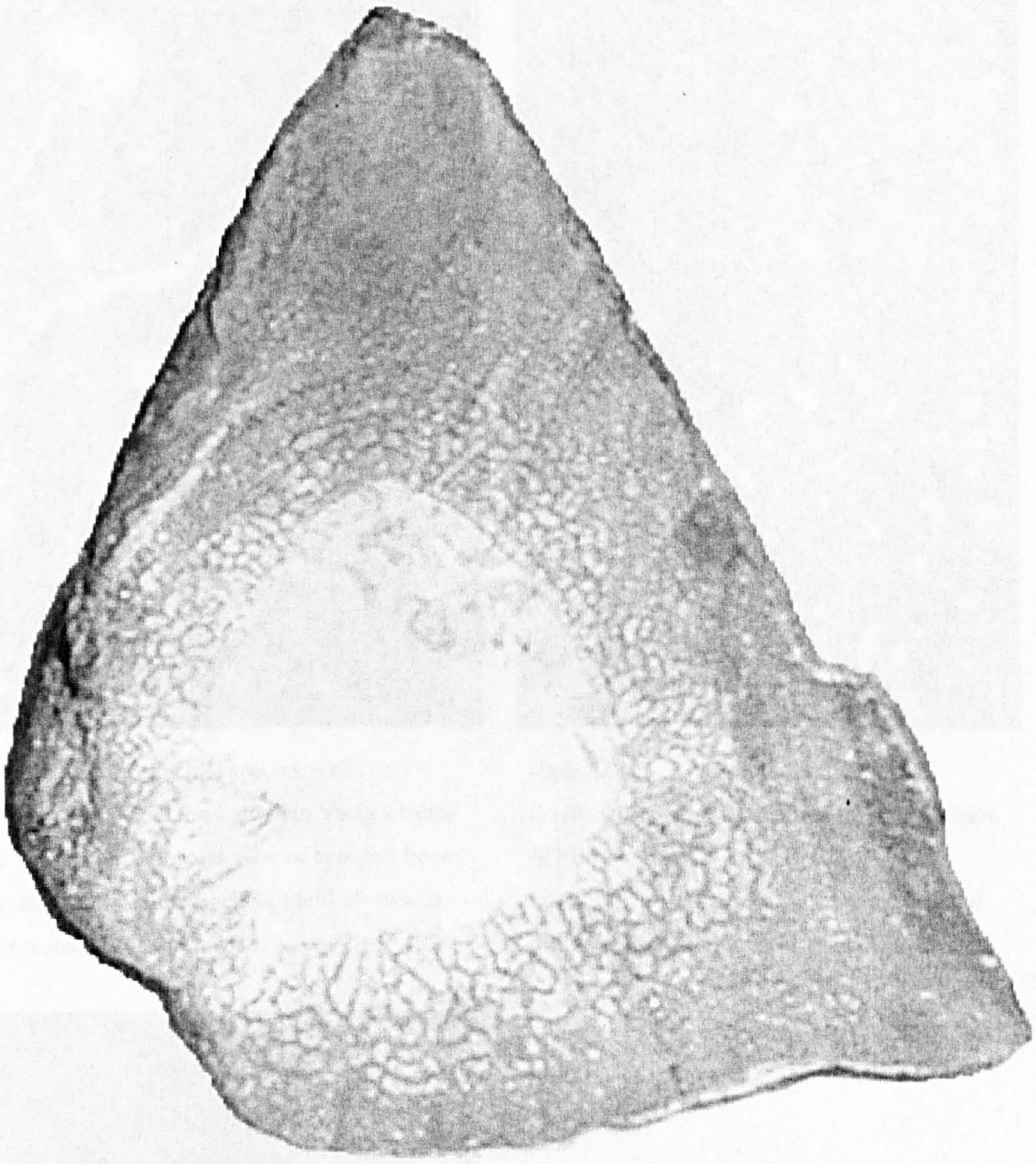


Figure 7.9. Branchial specimen of *Leedsichthys* from the Callovian Vaches Noire of Normandie. Ceratobranchial (48mm wide) cut to generate thin-section.

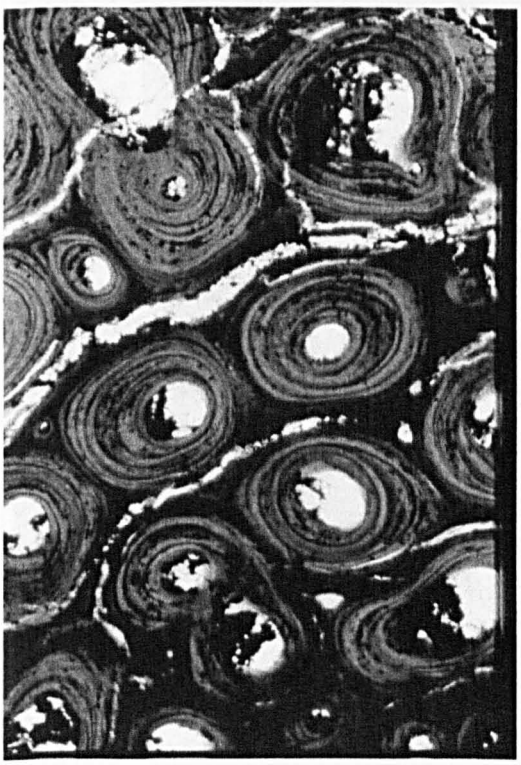


Figure 7.10a. Branchial specimen of *Leedsichthys* from the Callovian Vaches Noire of Normandie. General view of compact bone of sectioned ceratobranchial. Field-of-view is estimated at 1.7-2mm wide.

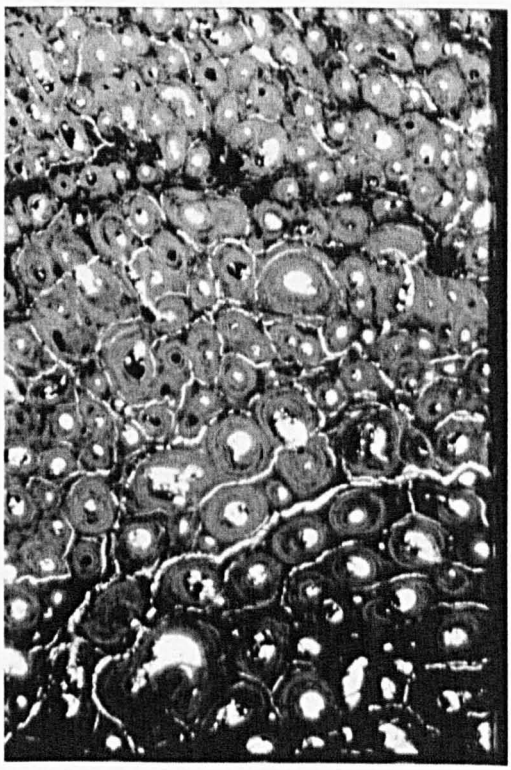


Figure 7.10b. Branchial specimen of *Leedsichthys* from the Callovian Vaches Noire of Normandie.
Detail of fig. 7.10a in PPL, showing vascular canals. Field-of-view is estimated at ~0.6mm.

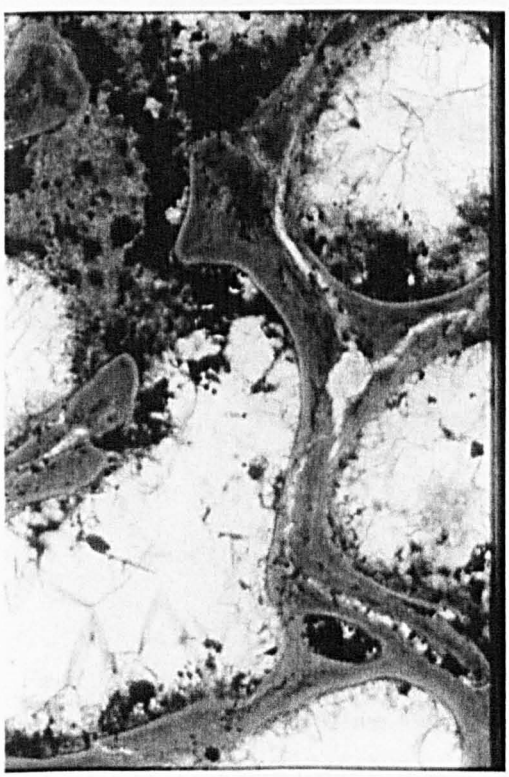


Figure 7.10c. Branchial specimen of *Leedsichthys* from the Callovian Vaches Noire of Normandie. Detail of fig. 7.10a in XPL, showing fibrolamellar bone forming osteons. Field-of-view is estimated at ~0.3mm.

Figure 7.11a. Branchial specimen of *Leedsichthys* from the Callovian Vaches Noire of Normandie. General view of cancellous bone, showing spongy cortex. Field-of-view is estimated at 1.7-2mm wide.

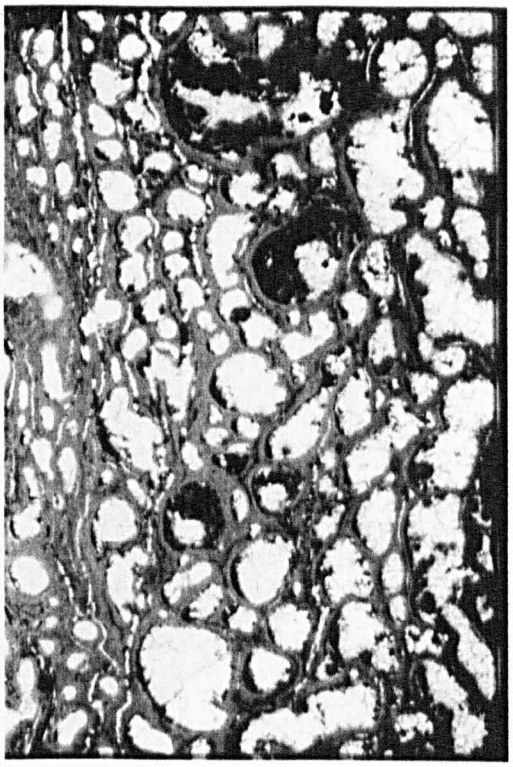


Figure 7.11b. Branchial specimen of *Leedsichthys* from the Callovian Vaches Noire of Normandie. Detail of cancellous bone, showing osteocytes and trabeculae. Field-of-view is estimated at ~0.3mm.

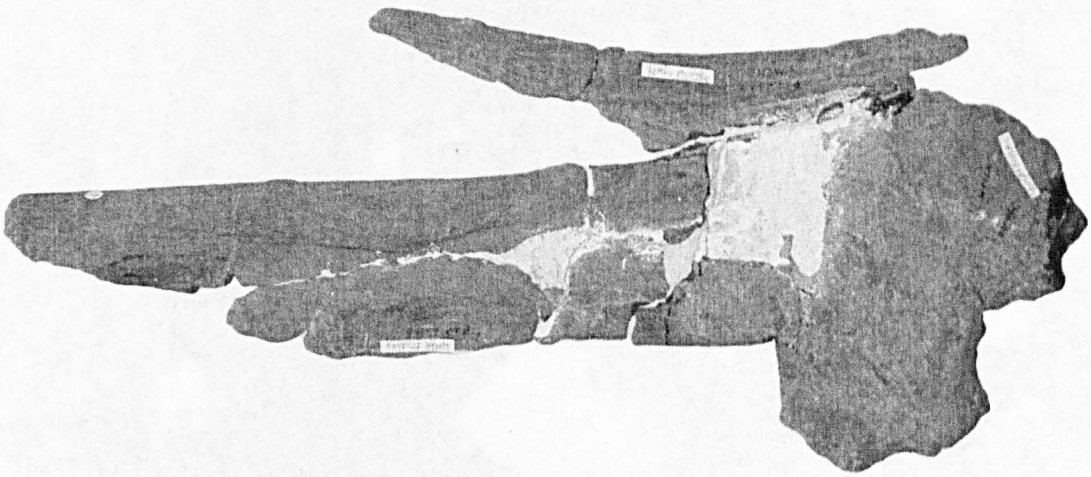


Figure 7.12. Branchial specimen (WmfN P20238) of *Leedsichthys* from the Callovian Ornatenton of Wiehengebirge. Specimen is 525mm long, has been repaired with plaster, and appears to be a ?epibranchial/ceratobranchial junction.

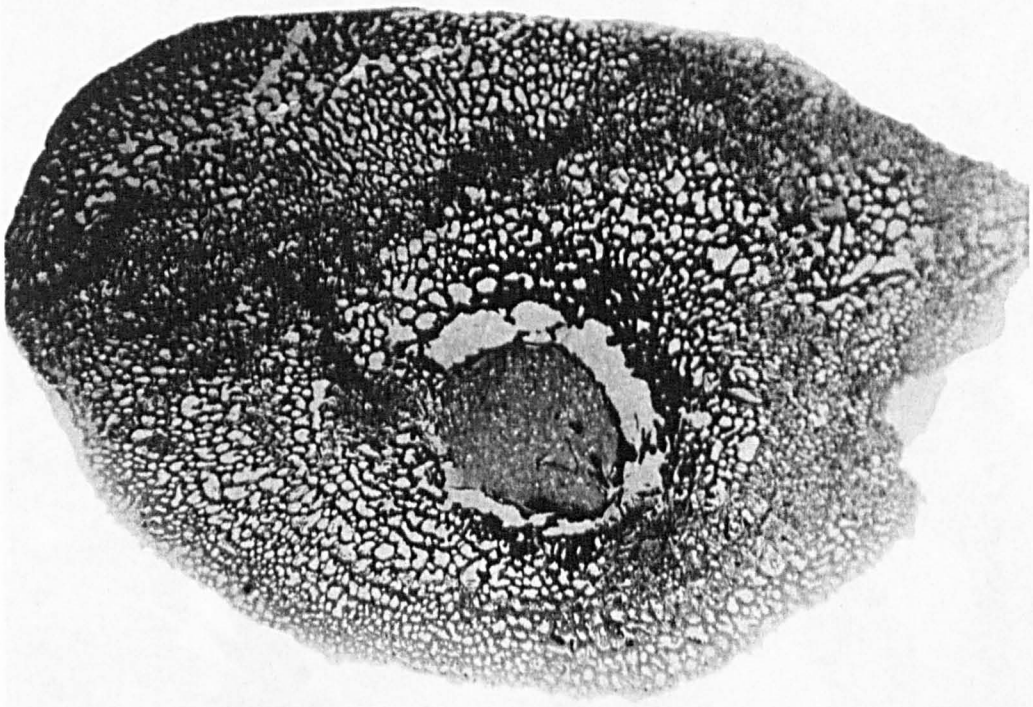


Figure 7.13. Branchial specimen of *Leedsichthys* from the Callovian Ornatenton of Wiehengebirge. Wallücke thin-section GLAHM 109519 from WmfN P20238. Field-of-view is 34mm in width.

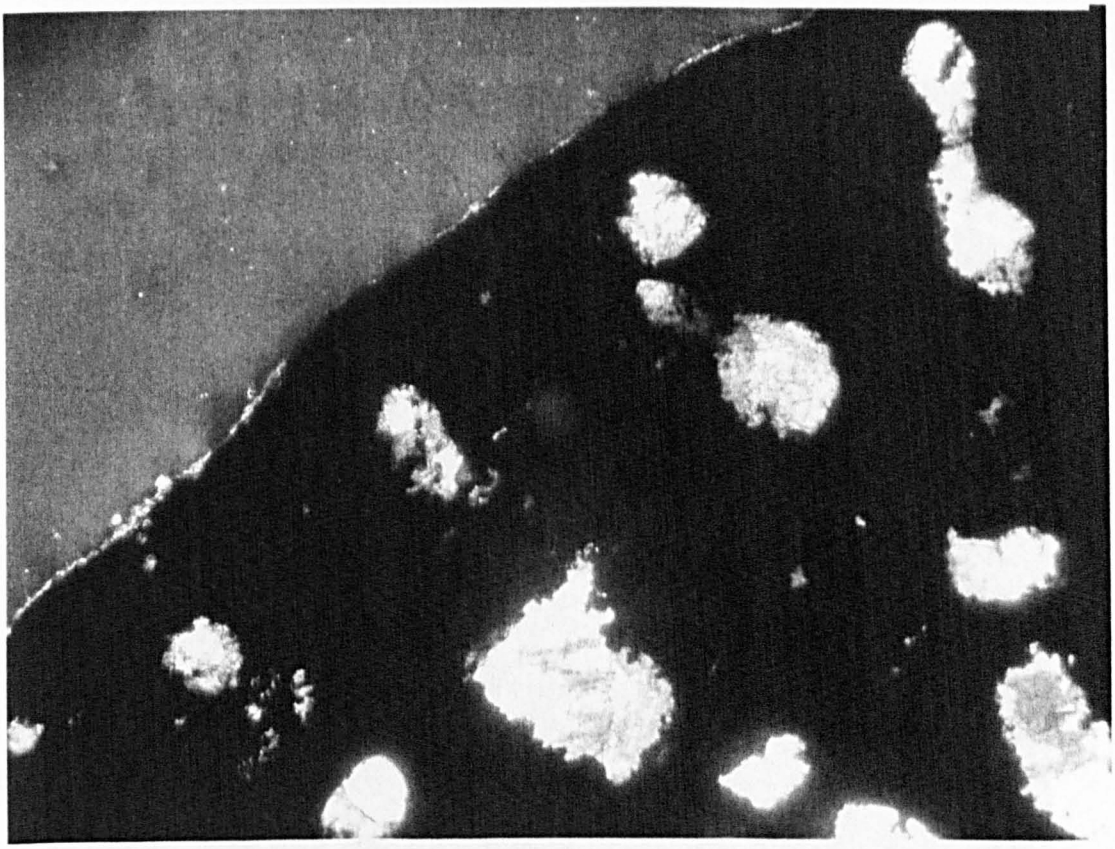


Figure 7.14. Branchial specimen of *Leedsichthys* from the Callovian Ornatenton of Wiehengebirge. Detail of section GLAHM 109519. Field-of-view = 1.5mm from lower right corner to surface of bone (top left of image), showing compact bone presence at surface of bone.

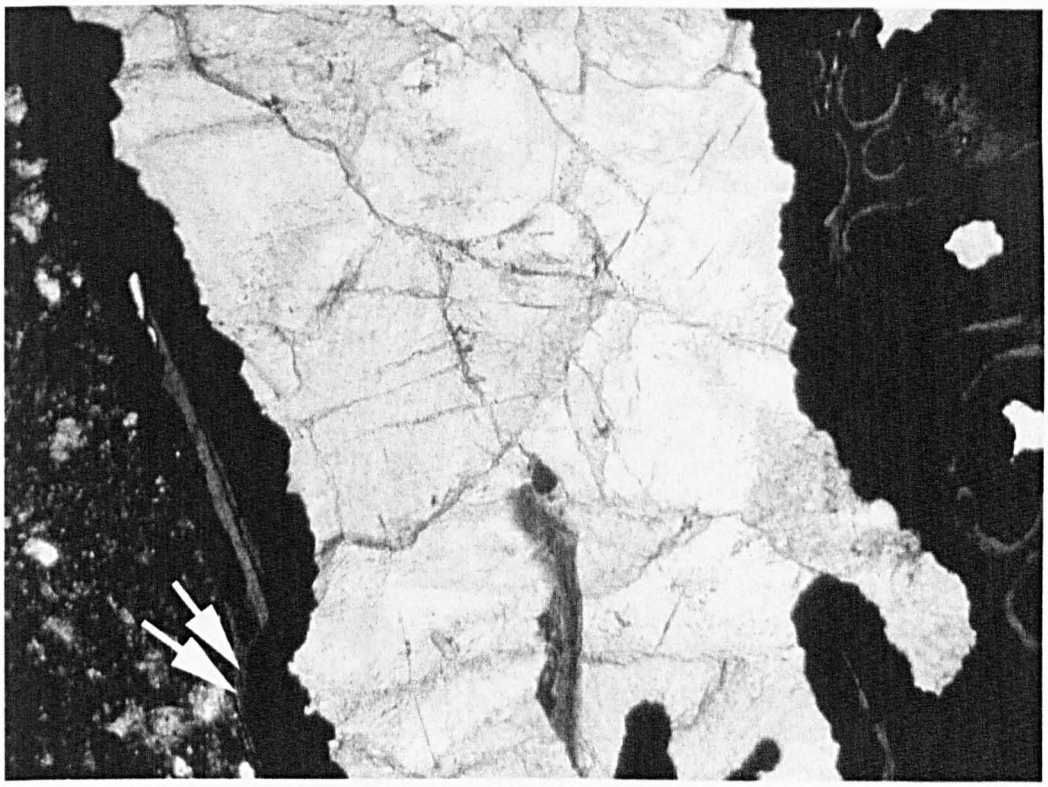


Figure 7.15. Branchial specimen of *Leedsichthys* from the Callovian Ornatenton of Wiehengebirge. Detail of section GLAHM 109519, showing intertrabecular space with marks of skeletal growth indicated by arrows. Field-of-view = 2mm wide.

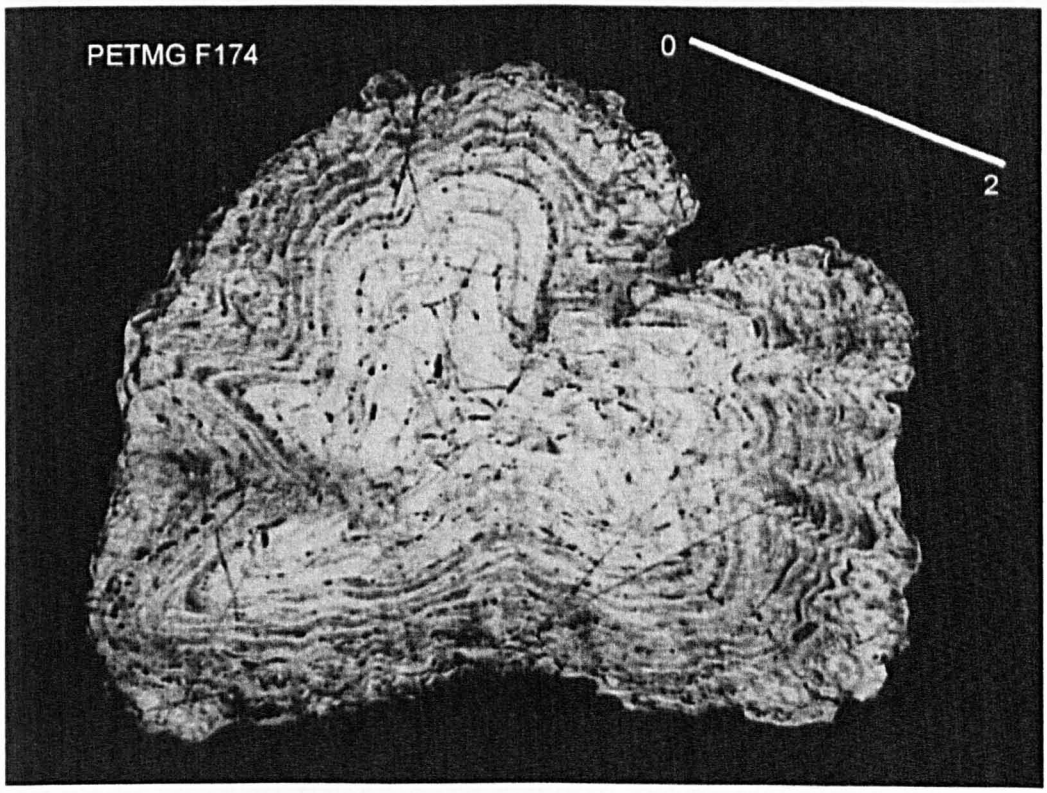


Figure 7.16. Polished section of 'Ariston' (PETMG F174), lepidotrichium with 21 annuli. Scale = 2mm.

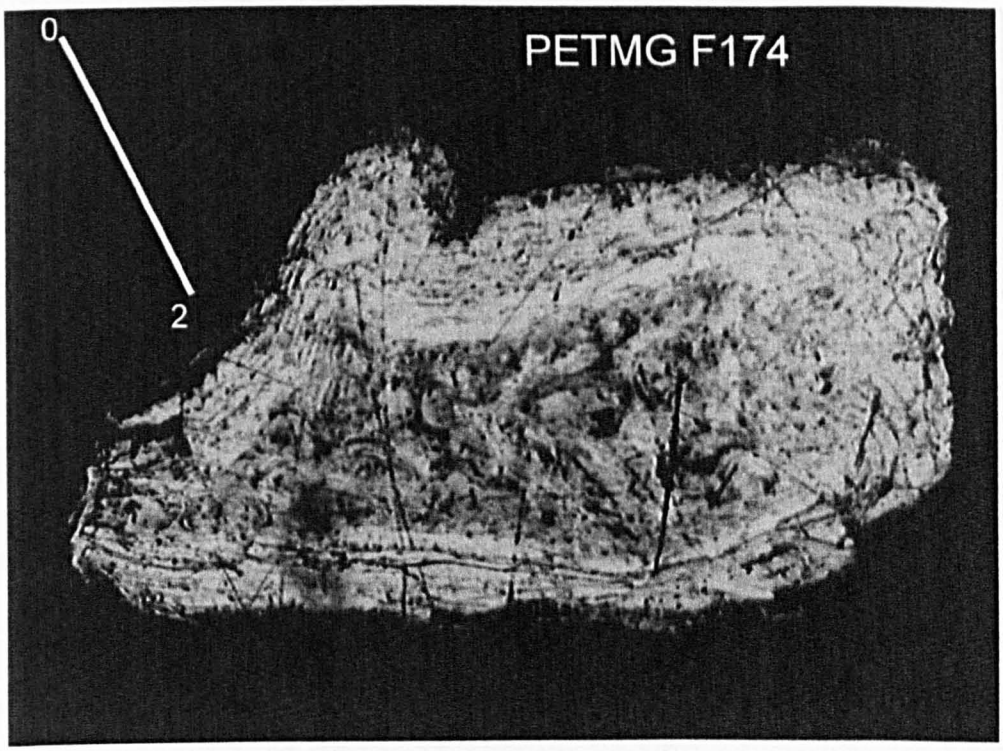


Figure 7.17. Polished section of 'Ariston' (PETMG F174), gill raker with 17 annuli and internal bone remodelling. Scale = 2mm.

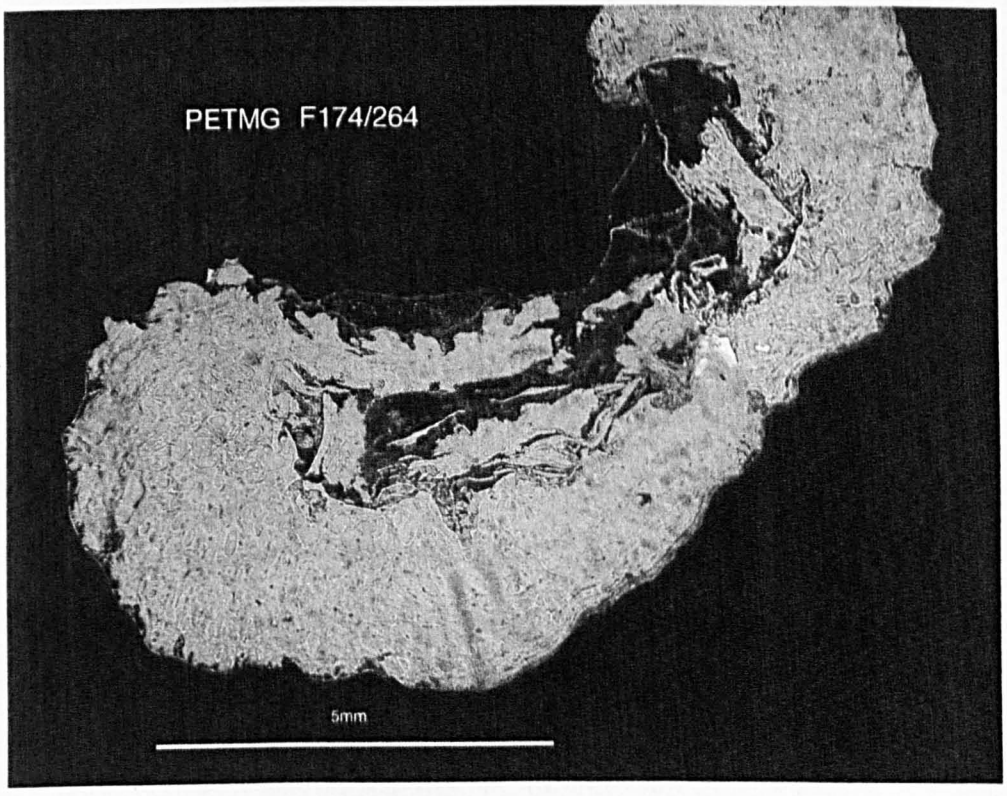


Figure 7.18. Polished section of 'Ariston' (PETMG F174), PETMG F174/264, meristic element, showing extensive internal remodelling. Scale = 5mm.

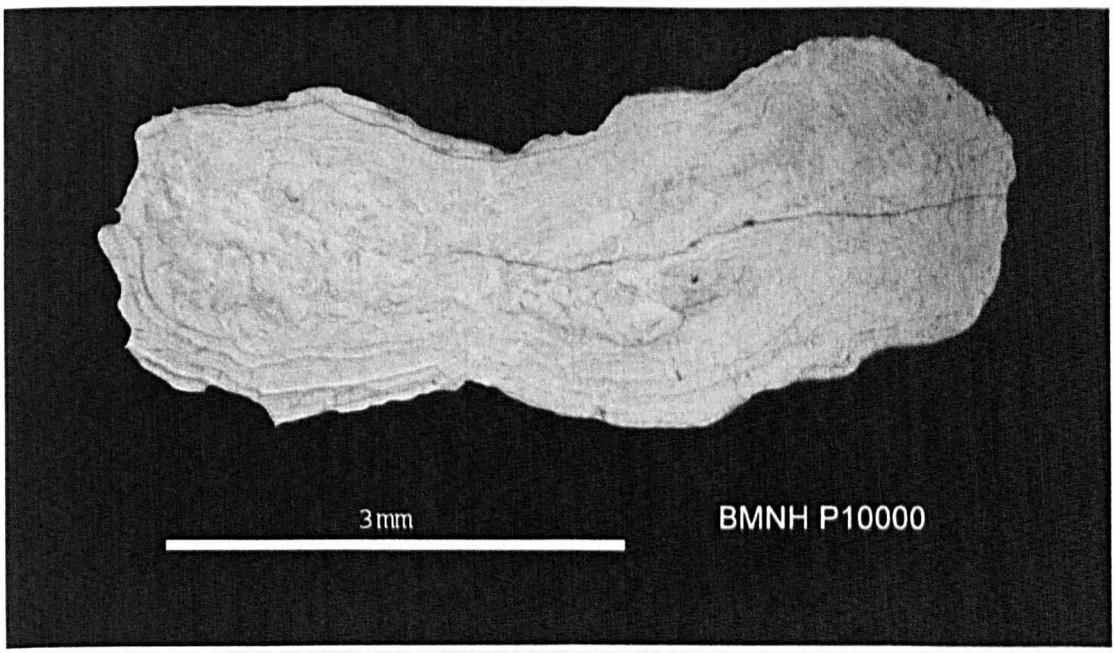


Figure 7.19. Polished section of 'Tail specimen' (BMNH P.10,000) gill raker with 19 annuli and inner bone remodelling. Scale = 3mm.

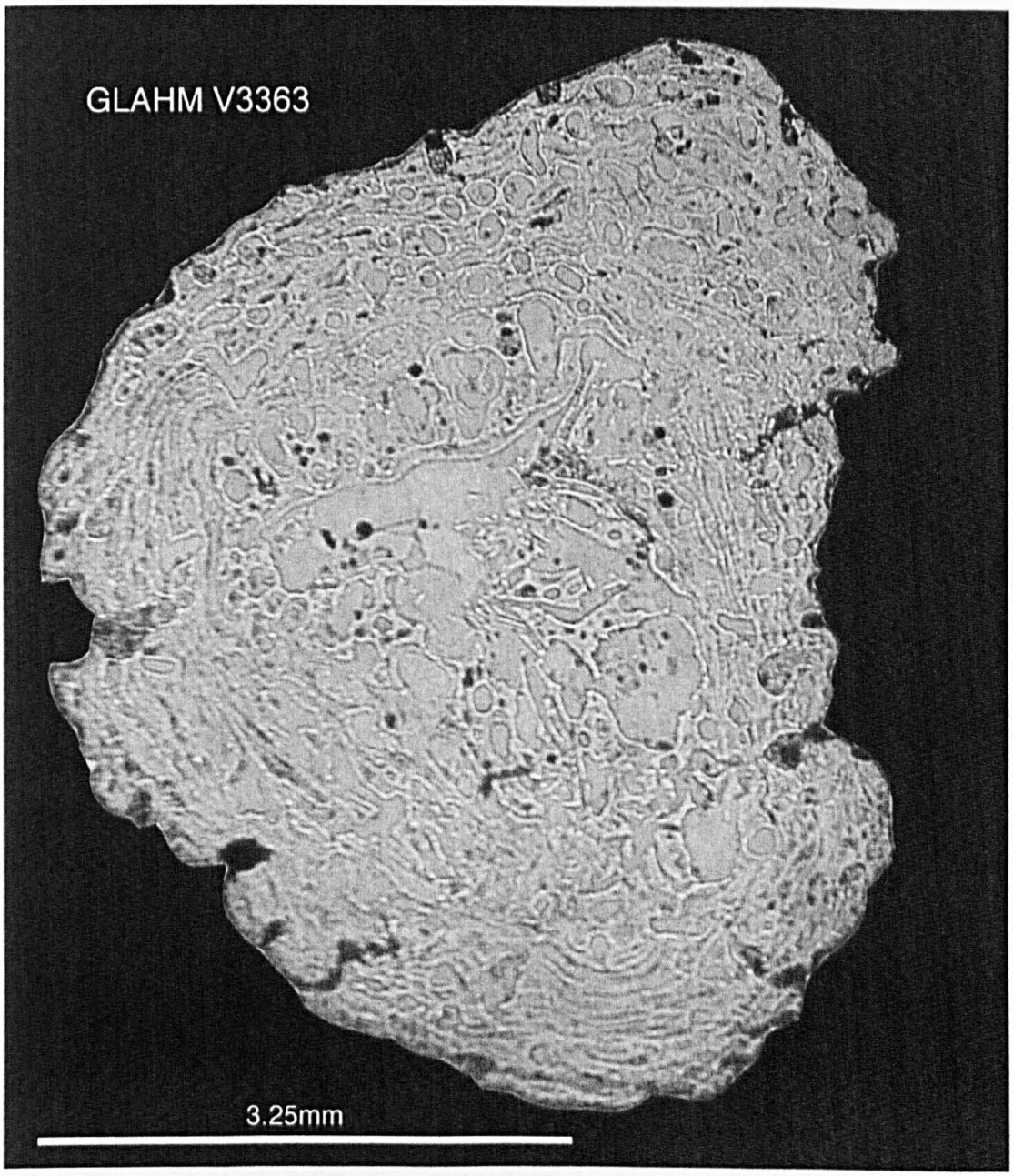


Figure 7.20. Polished section of 'Big Meg' (GLAHM V3363) meristic element, showing 15 annuli and inner bone remodelling. Scale = 3.25mm.

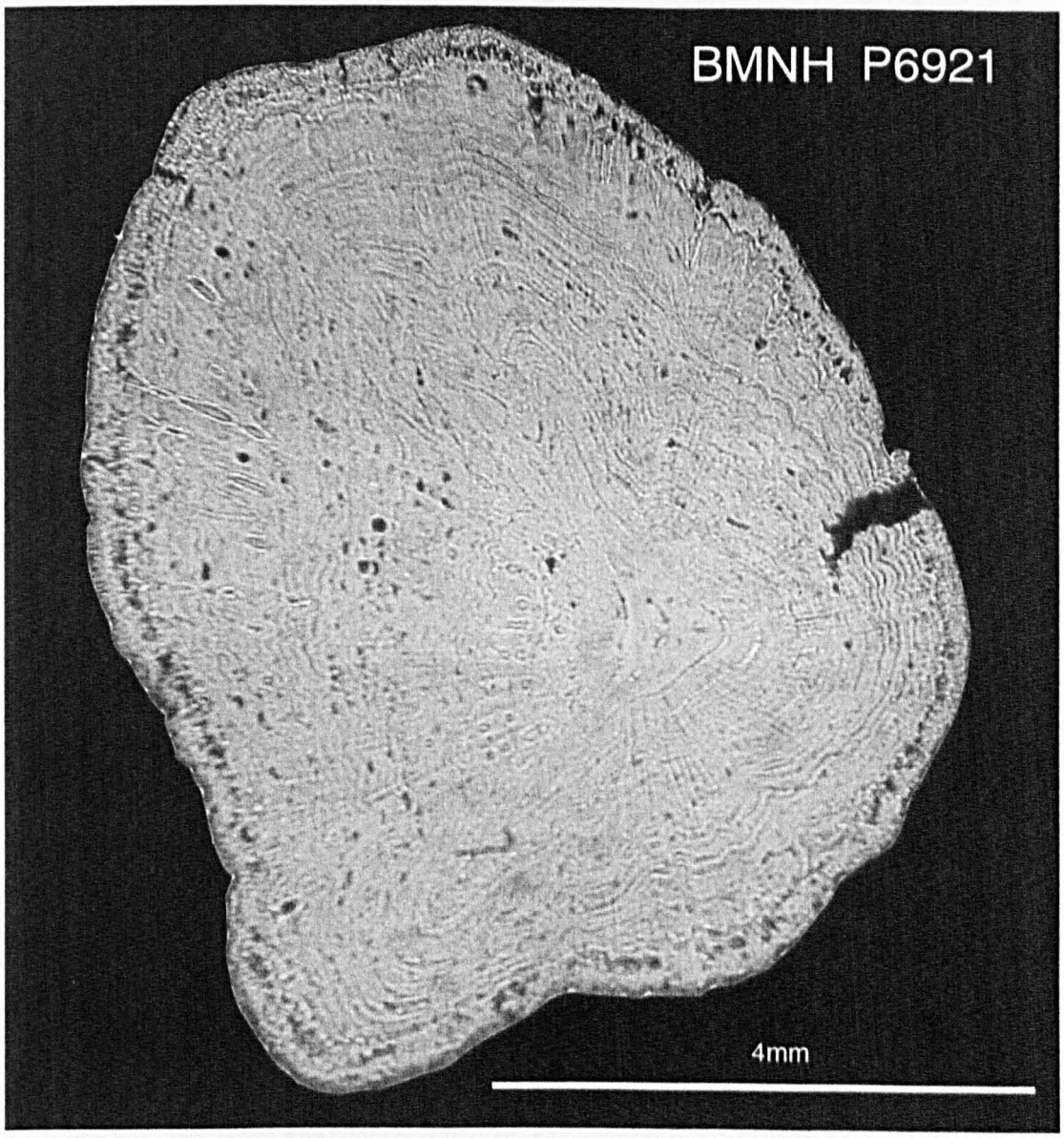


Figure 7.21a. Polished section of Holotype (BMNH P.6921) lepidotrichium with 40 annuli. Scale = 4mm.

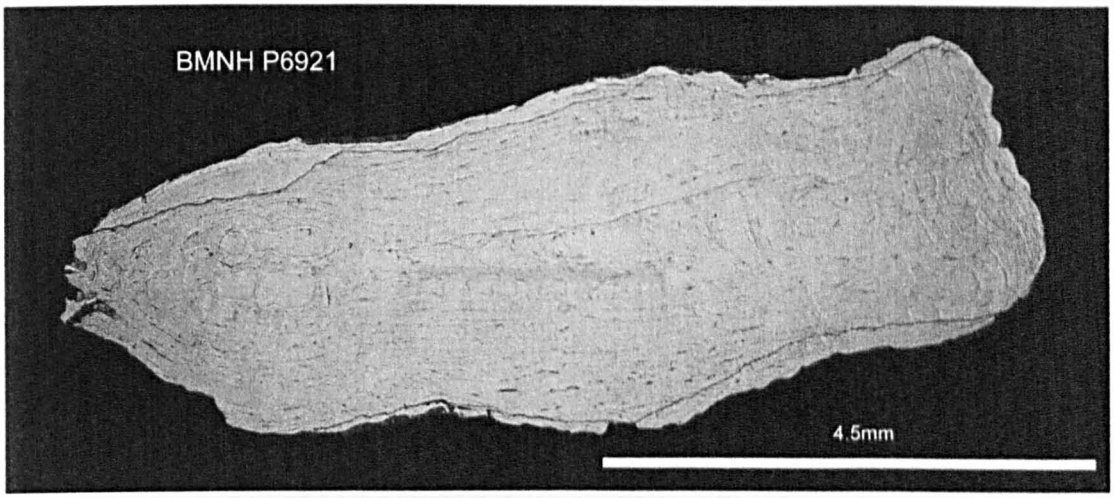


Figure 7.21b. Polished section of Holotype (BMNH P.6921) gill raker with 33 annuli and inner bone remodelling. Scale = 4.5mm.

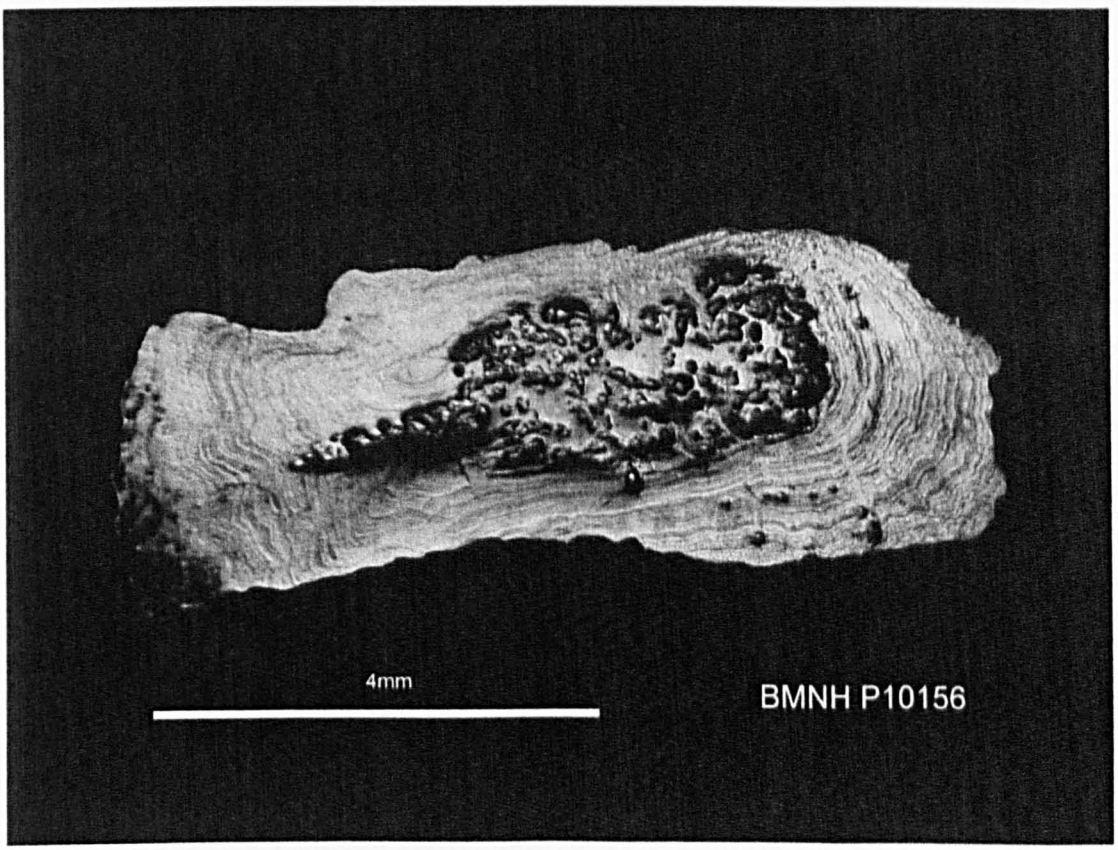


Figure 7.22. Polished section of 'Gill Basket specimen' (BMNH P.10156) gill raker with 37 annuli, extensive bone remodelling and pyrite infill. Scale = 4mm.

Figure 7.23 - Linear plot of Holotype Lepidotrichium - NE Transect

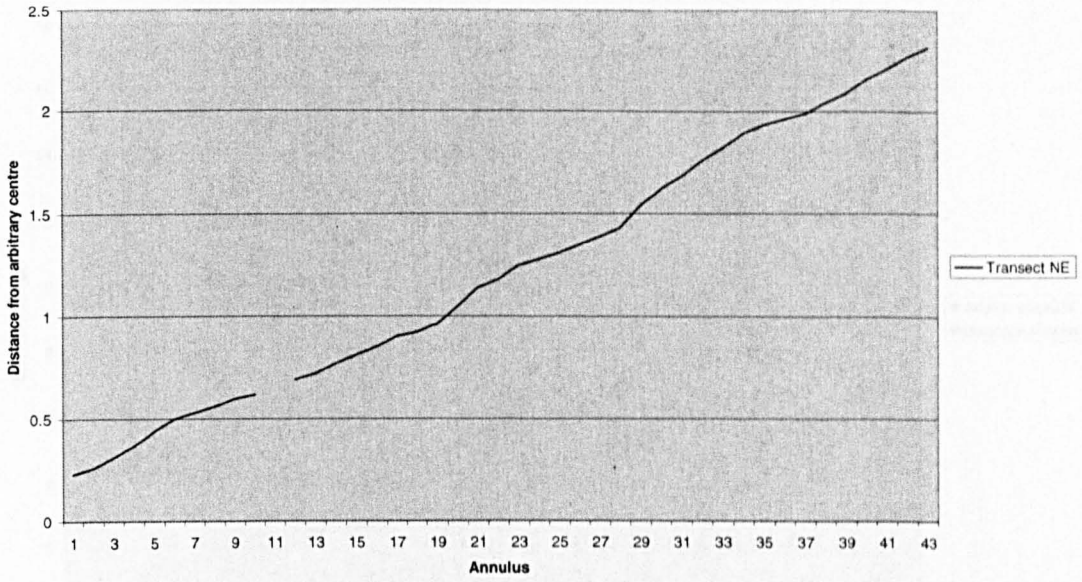


Figure 7.23. Linear plot of Holotype (BMNH P.6921) lepidotrichium annuli.

Figure 7.24 - Walford-Ford plot of Holotype Lepidotrichium - NE Transect

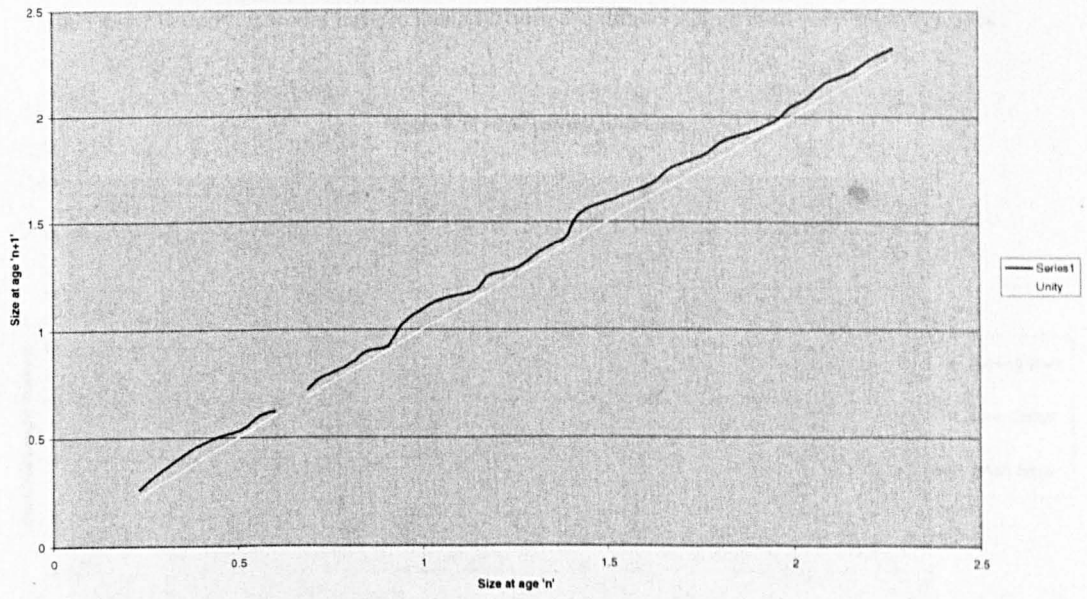


Figure 7.24. Walford-Ford plot of Holotype (BMNH P.6921) lepidotrichium annuli.

Figure 7.25 - Application of single element growth intercept to total animal growth

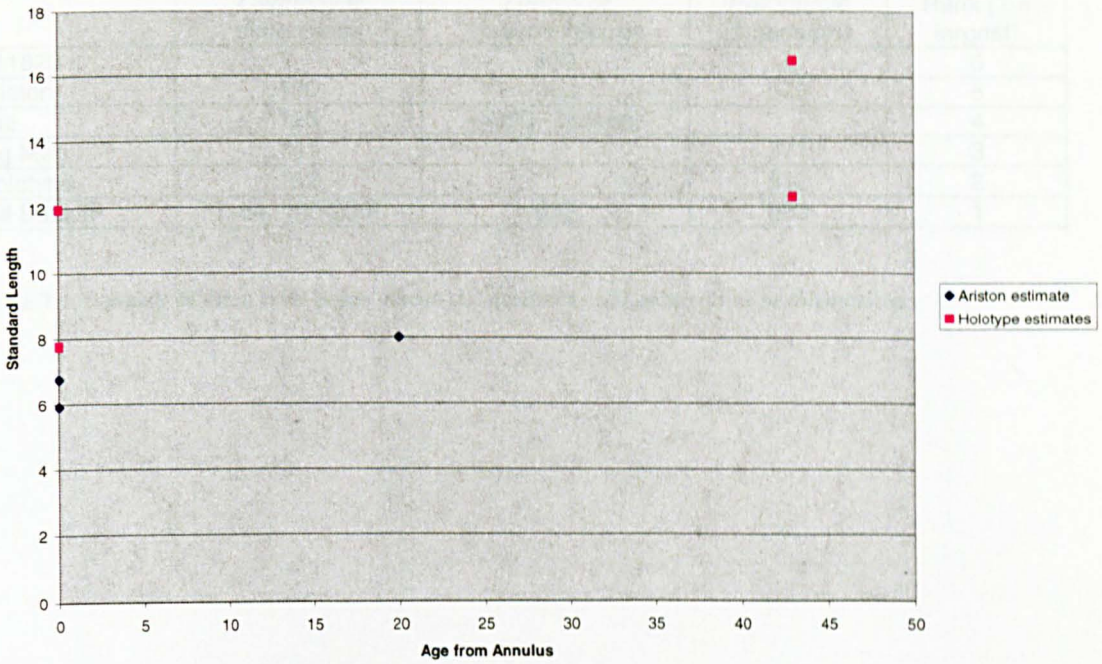


Figure 7.25. Examples of extrapolated growth using gradients from growth of individual elements as equivalent for gradients of growth of whole animal, for 'Ariston' and the Holotype. If *Leedsichthys* only grew linearly, it would have to hatch/be born at extremely large (and very unlikely) sizes.

Figure 7.26 - Comparison of Growth

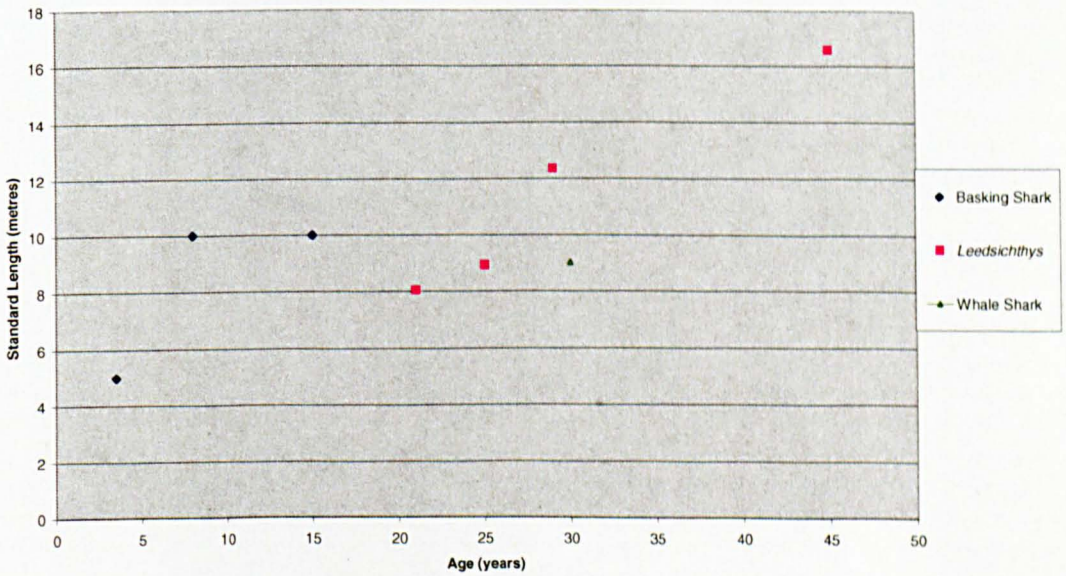


Figure 7.26. Graph of estimated sizes for *Rhincodon typus* (whale shark), *Cetorhinus maximus* (basking shark) and *Leedsichthys problematicus* plotted together for comparison.

Chapter 7: Tables.

	Ceratohyal dimensions	*Length of hyomandibula*	*Preopercle dimensions*	Rank (1 = largest)
P11823		530		6
Ariston	100	663	575	5
Tail	125	[>650 - broken]		4
Big Meg	141		771	3
Holotype	152		812	2
Gill Basket	[>84, 160-230]	687	820	1

Table 7.1. Ranking of three skull bones across six specimens of *Leedsichthys problematicus*.

Table 7.2. Annuli Measurements (all in mm).

Annulus Number (uncompensated)	PETMG F174 LPDT	PETM G F174 GR	BMNH P10000 GR	GLAHM V3363 ME	BMNH P6921 GR	BMNH P6921 LPDT	BMNH P10156 GR
1	0.33	1.37	0.51	1.88		0.98	
2	0.59	1.57	0.68	1.95			
3	0.94	1.62	0.74	2.00		1.80	1.23
4	1.09	1.71	0.81	2.05	2.71	1.90	1.32
5	1.24	1.78	0.87	2.11	2.78	1.98	1.39
6	1.28	1.84	0.98	2.15	2.86	2.04	1.43
7	1.35	1.98	1.06	2.22	2.95		1.46
8	1.50	2.07	1.22	2.27	3.21	2.24	1.56
9	1.65	2.16	1.34	2.34	3.29	2.40	1.63
10	1.72	2.24	1.63	2.41	3.62	2.49	1.78
11	1.82	2.29	1.90	2.45	3.72	2.62	1.88
12	1.89	2.41	2.03	2.56	3.84	2.72	2.02
13	2.01	2.49	2.12	2.63	3.89		2.09
14	2.06	2.53	2.15	2.68	3.98		2.18
15	2.10	2.59	2.23	2.73	4.04	2.87	2.24
16	2.18	2.67	2.31		4.14		2.32
17	2.26	2.72	2.33		4.20	3.01	2.38
18	2.37		2.45		4.24		2.42
19	2.44		2.52		4.29		2.60
20	2.65				4.36	3.14	2.66
21	2.77				4.41	3.19	2.71
22					4.45	3.24	2.75
23					4.48	3.30	2.77
24					4.51	3.35	2.80
25					4.54		2.87
26					4.59		2.91
27					4.63		3.02
28					4.69		3.07
29					4.73		3.11
30					4.78		3.16
31					4.83		3.26
32					4.89		3.30
33					4.95		3.36
34						3.53	3.37
35						3.61	3.41
36						3.70	3.46
37						3.83	3.51
38						3.90	3.55
39						3.99	
40						4.03	
41							
42							
43							
44							
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51							
52							
53							

Table 7.3. Comparison of size and age estimations for five specimens of *Leedsichthys*.

	Ariston PETMG F174	Tail BMNH P.10000	Big Meg GLAHM V3363	Holotype BMNH P.6921	Gill Basket BMNH P.10156
Estimated Length	8.0m	8.9m	12.3m		16.5m
Raker Thickness	6.15mm	6.00mm		8.56mm	8.00mm
LpdT Thickness	4.78mm		4.66mm	6.76mm	
Maximum ring no. Gill Raker	17	19		33	38
Maximum ring no. LpdT	21		15, with extensive resorption	40	
Estimated Resorbed	4	~6	~12-16	~7	~7
Estimated Age (yrs)	21	25	27-31	40	45

Chapter 8: Figures

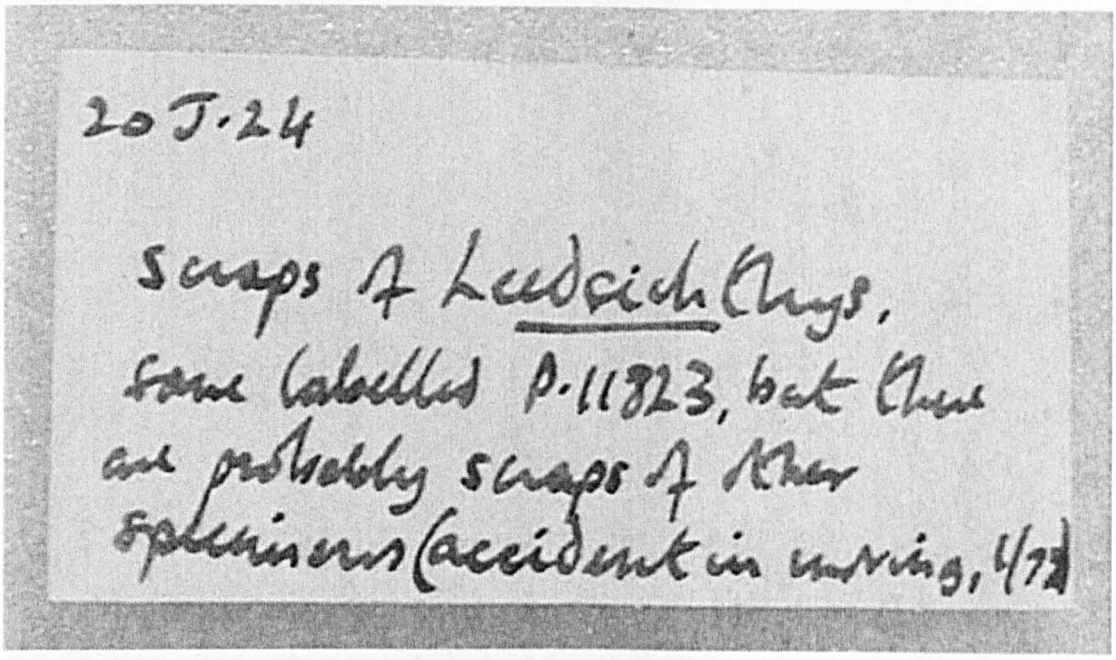


Figure 8.1. Label with BMNH P.11823, referring to January 1972 accident.

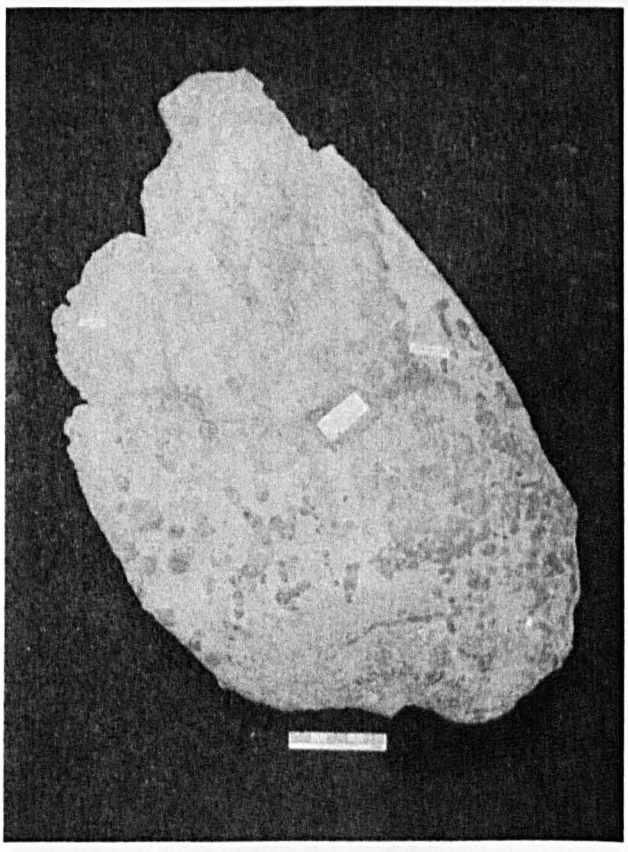


Figure 8.2a. CAMSM J.46874 stegosaur armour from the Oxford Clay, noted by Harry Govier Seeley on 25/8/1898. Lateral view. Scale bar = 50mm.

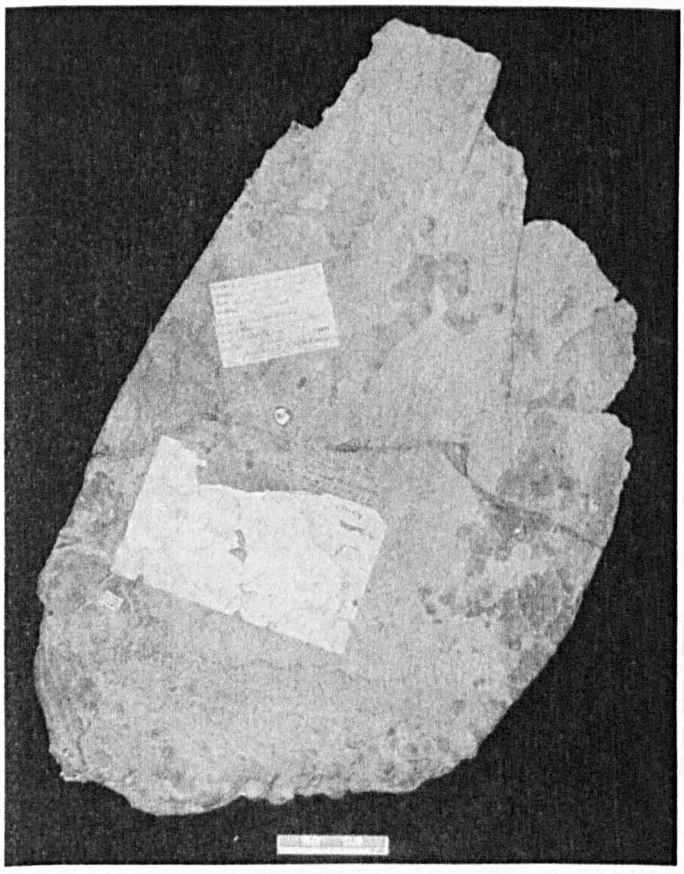


Figure 8.2b. CAMSM J.46874, medial view. Note smoothness of surface, and uniformity of striation direction. Scale bar = 50mm.

Figure 8.2c. CAMSM J.46874, showing the solid broad base, in contrast with the fractured 'diploë' evident with *Leedsichthys* parietals. Scale bar = 50mm.

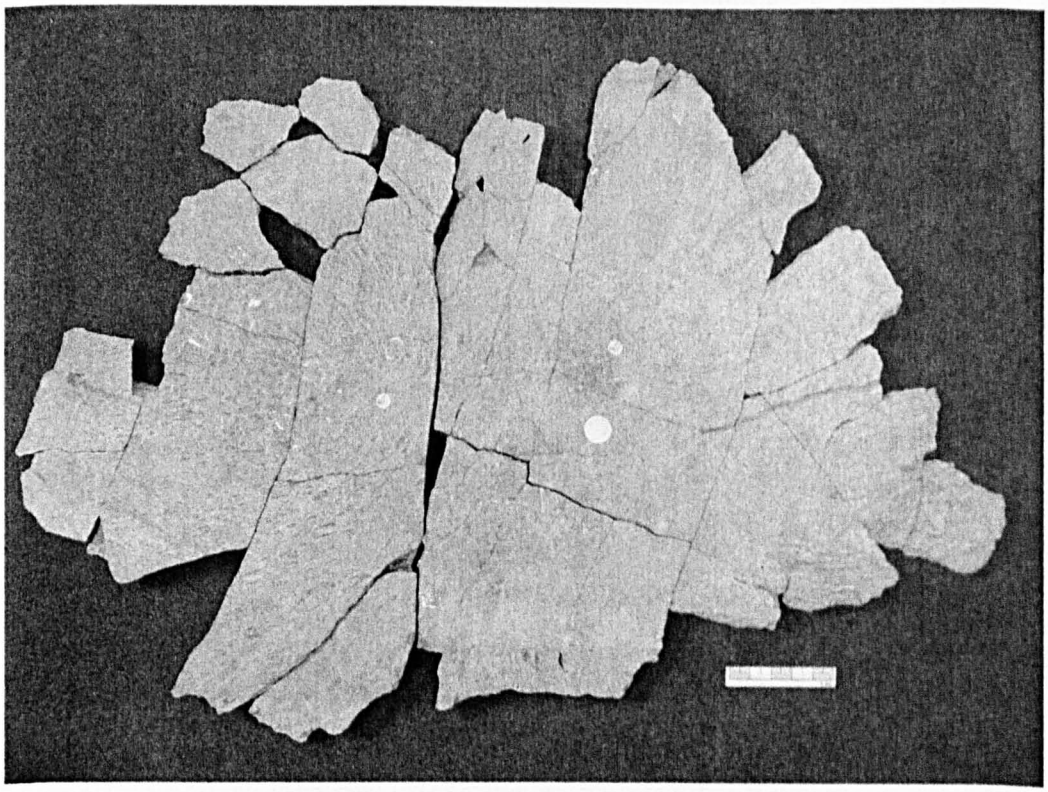


Figure 8.3a. BMNH P.6921 left ?parietal, 449mm x 311mm, dorsal surface. Scale bar = 50mm.

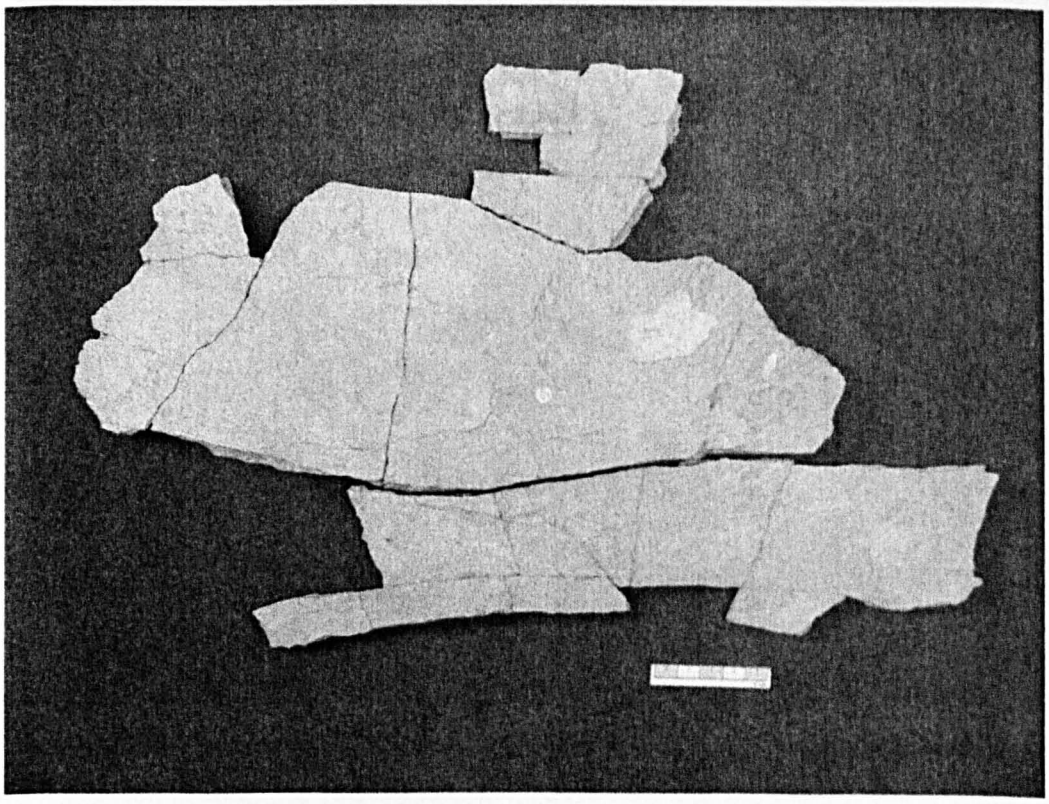


Figure 8.3b. BMNH P.6921 parietal, 411mm x 288mm, dorsal surface. Scale bar = 50mm.

Figure 8.4. CAMSM J.67420 right parietal, 211mm x 98mm, dorsal surface. Scale bar = 50mm.

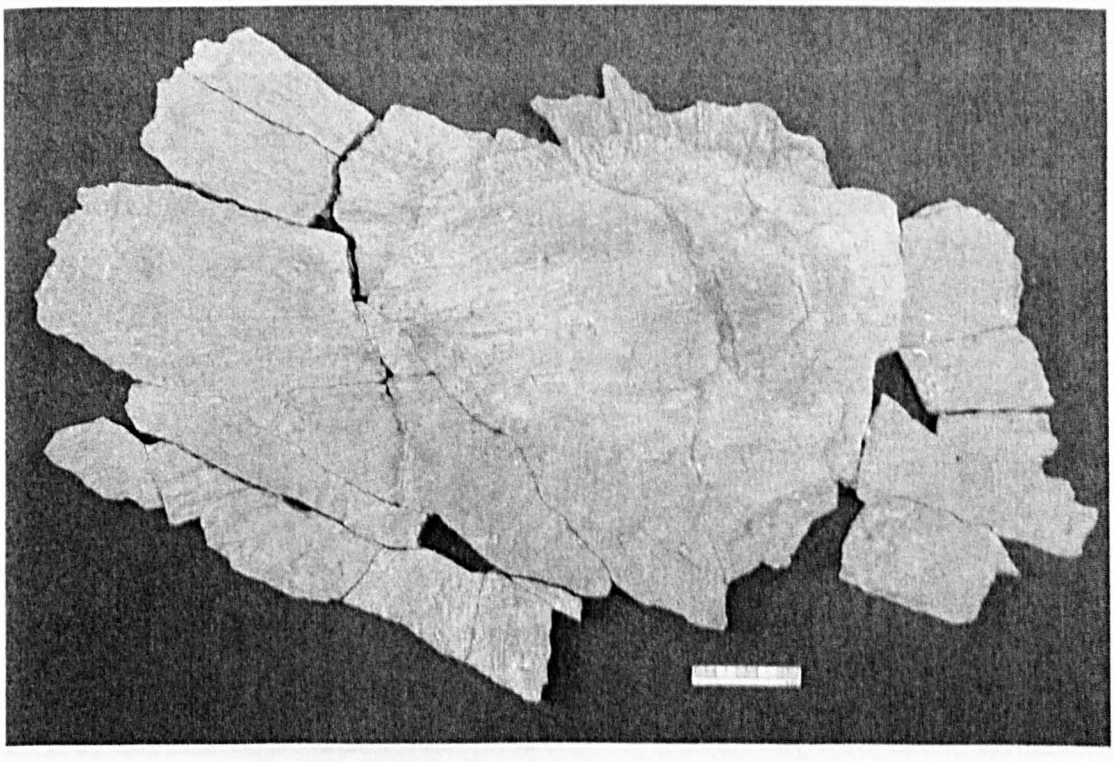


Figure 8.5. GLAHM V3363, right parietal, 515mm long, dorsal surface. Scale bar = 50mm.

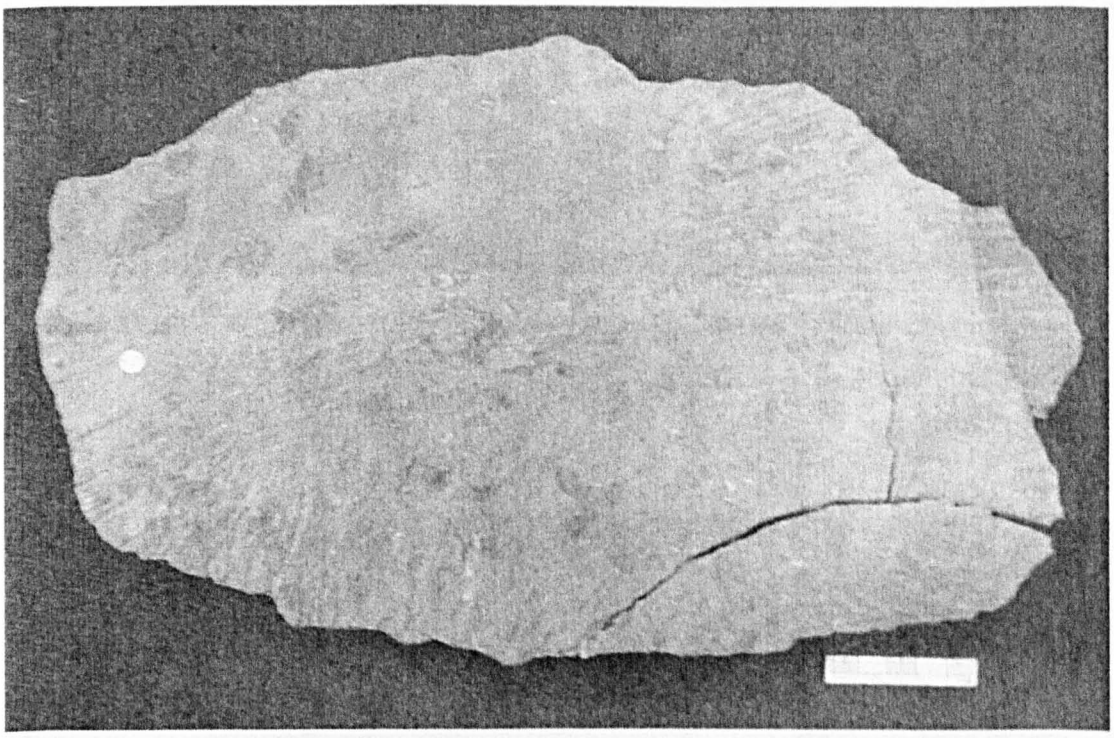


Figure 8.6. BMNH P.11824 right parietal, 387mm long, dorsal surface. Scale bar = 50mm.

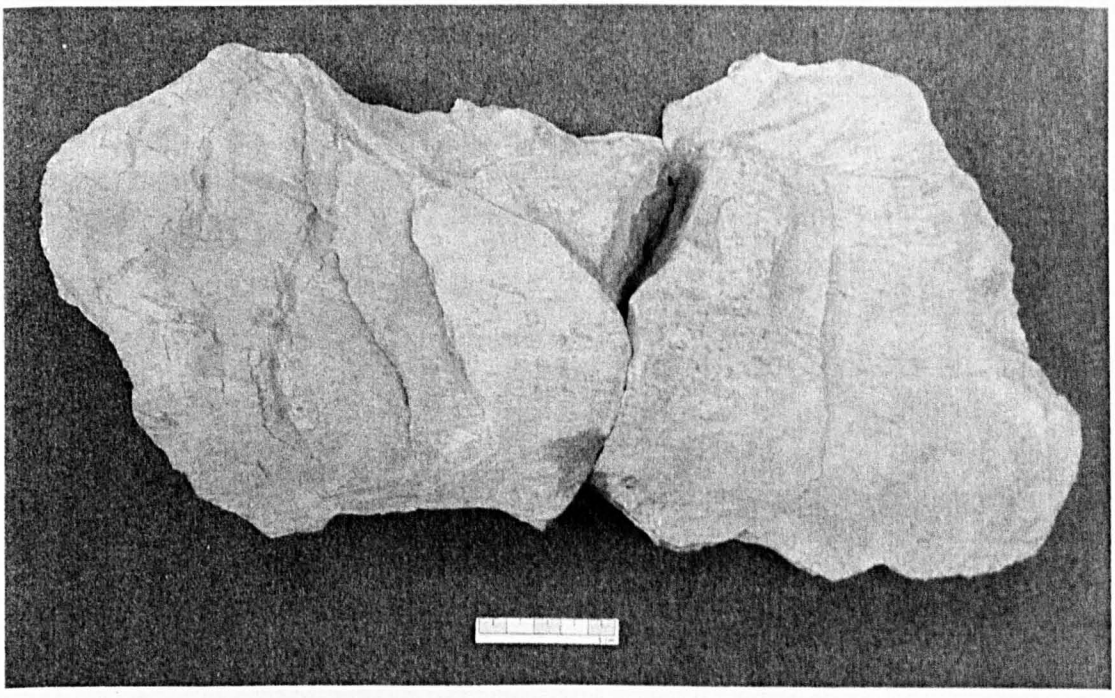


Figure 8.7. LEICT G128.1900 left parietal, 381mm long, dorsal surface. Scale bar = 50mm.

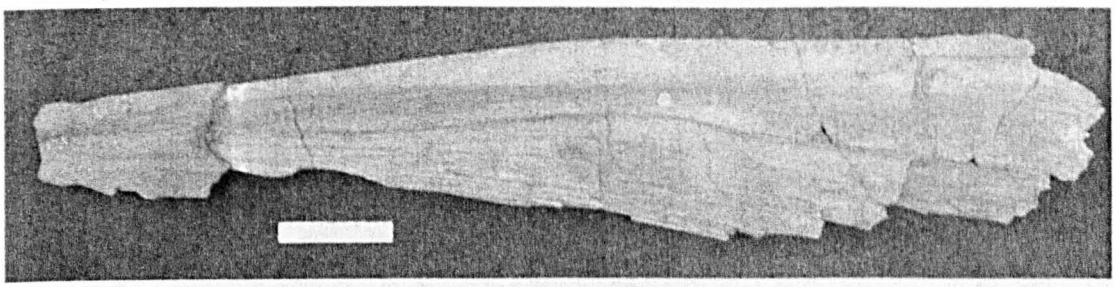


Figure 8.8a. BMNH P.6921 left cleithrum, 511mm long, external surface. Scale bar = 50mm.

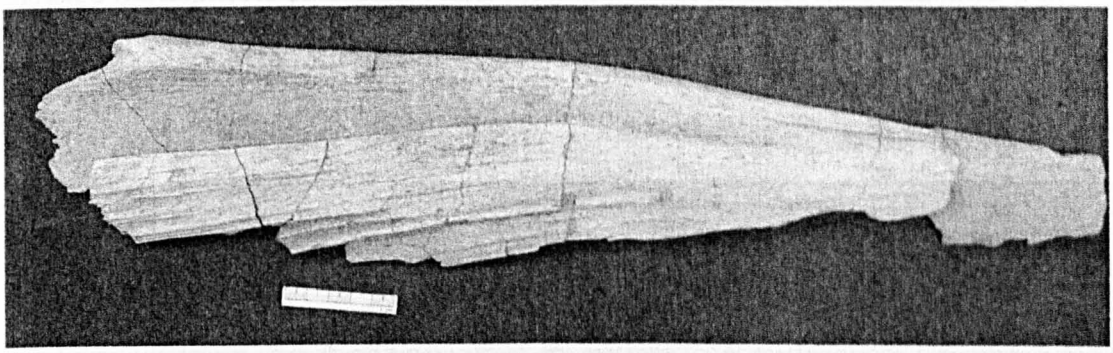


Figure 8.8b. BMNH P.6921 left cleithrum, 511mm long, internal surface. Scale bar = 50mm.

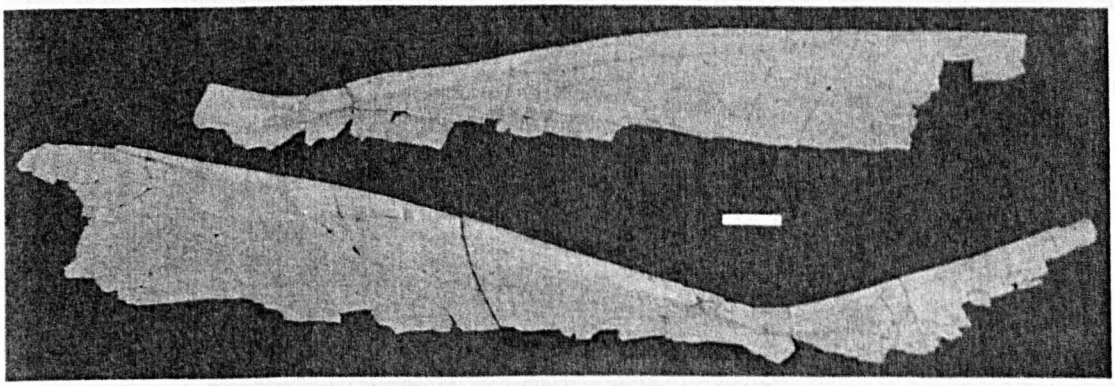


Figure 8.9. BMNH P.10000 left (upper) and right (lower) cleithrum, 782mm and 1017mm long respectively, external surfaces. Scale bar = 50mm.

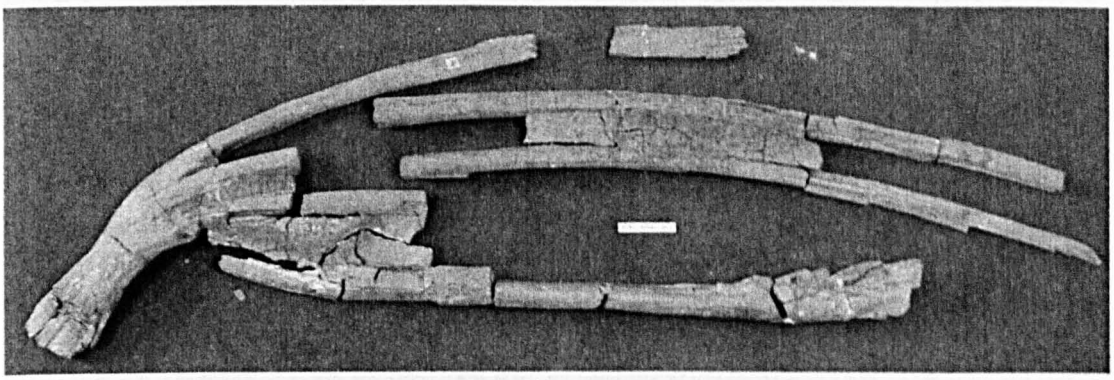
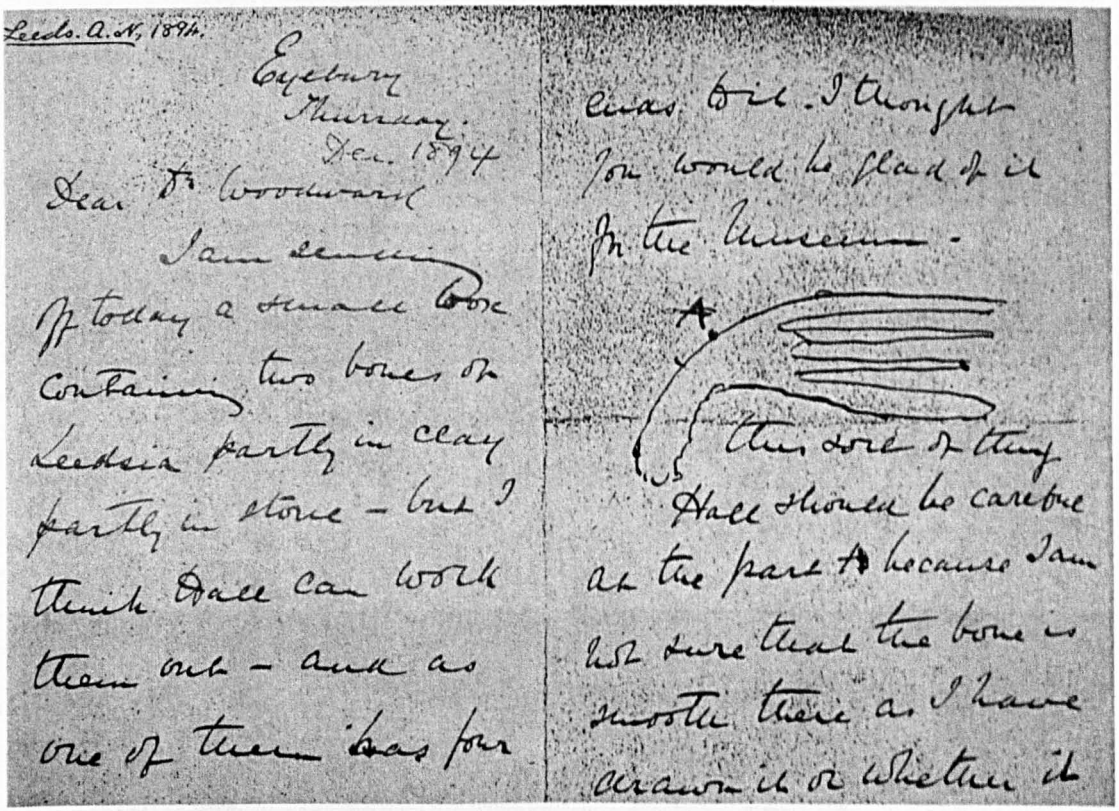


Figure 8.10a. BMNH P.6921(see section 8.3.1.7) branched meristic element, 821mm long, lateral view. Scale bar = 50mm.


Leeds. A. N. 1894.

Eyebury
Thursday.
Dec. 1894

Dear Dr Woodward

I am sending
by today a small box
containing two bones of
Leedsia partly in clay
partly in stone – but I
think Hall can work
them out – and as
one of them has four

cross bit. I thought
you would be glad of it
for the museum –

the end of the thing
Hall should be careful
at the part A because I am
not sure that the bone is
smooth there as I have
drawn it or whether it

Figure 8.10b. Letter from Alfred Leeds to Arthur Smith Woodward dated December 1894, with a sketch of a bone that he has just recovered for further preparation by Hall of the BM(NH). As BMNH P.6921 went with the 'First Collection' between 1889 and 1892, and this sketch bears a striking resemblance to the bone figured above (which is unique within the hypodigm), this specimen may not actually be a part of the type material for *Leedsichthys problematicus*. It may have suffered misassociation during specimen movement.

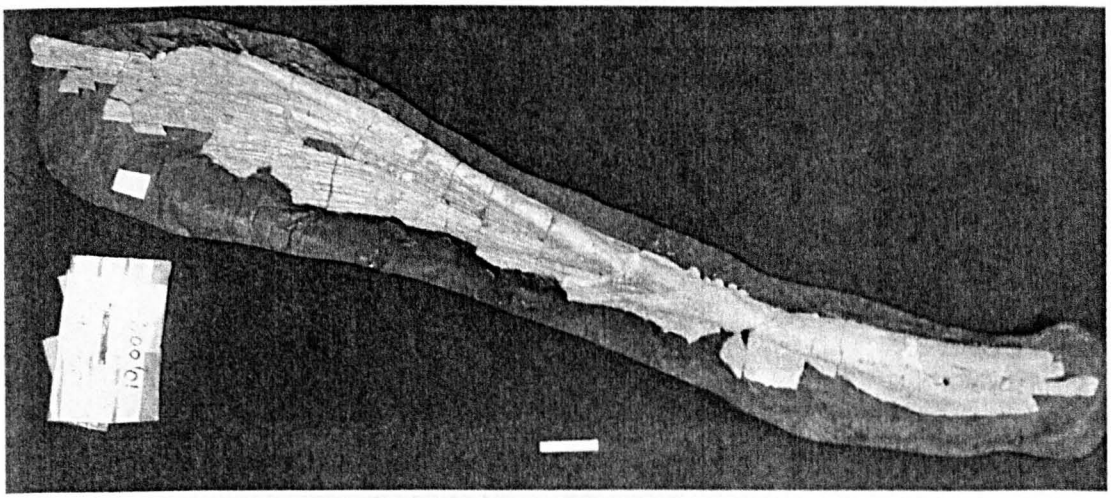


Figure 8.11. PETMG F.174/10004 right cleithrum, 1047mm long, external surface. Scale bar = 50mm.

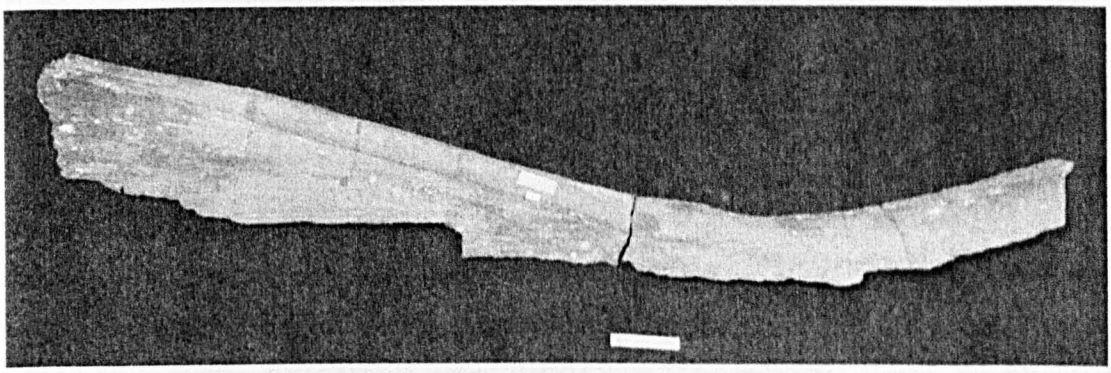


Figure 8.12. CAMSM X.50112 right cleithrum, 836mm long, external surface. Scale bar = 50mm.

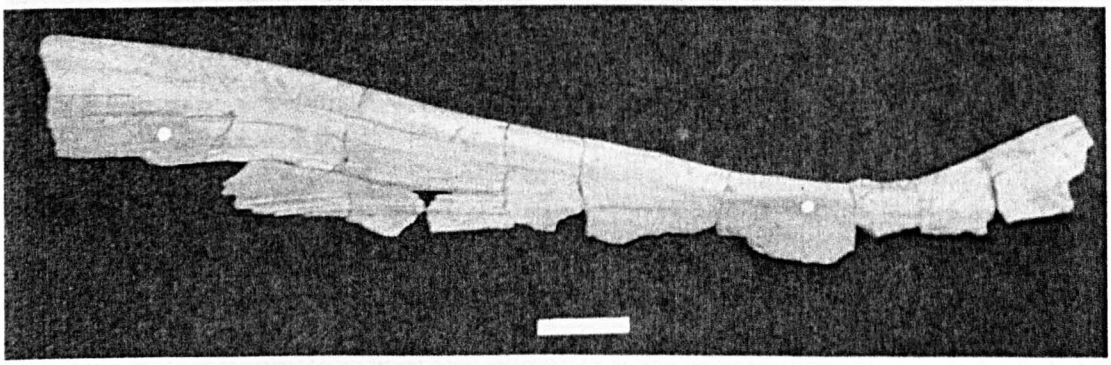


Figure 8.13. BMNH P.8609 right cleithrum, 625mm long, external surface. Scale bar = 50mm.

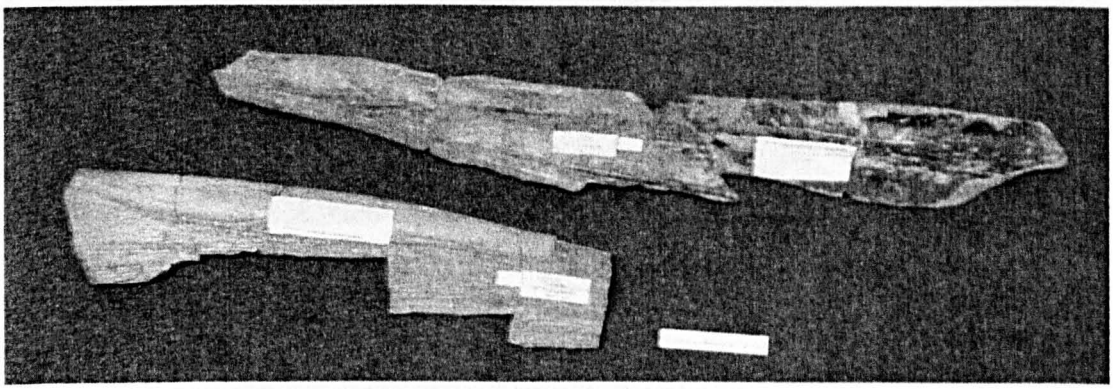


Figure 8.14. CAMSM J.67475 ?left cleithrum (above, 418mm long) with (below) right cleithrum (258mm long), external surfaces of both. Scale bar = 50mm.

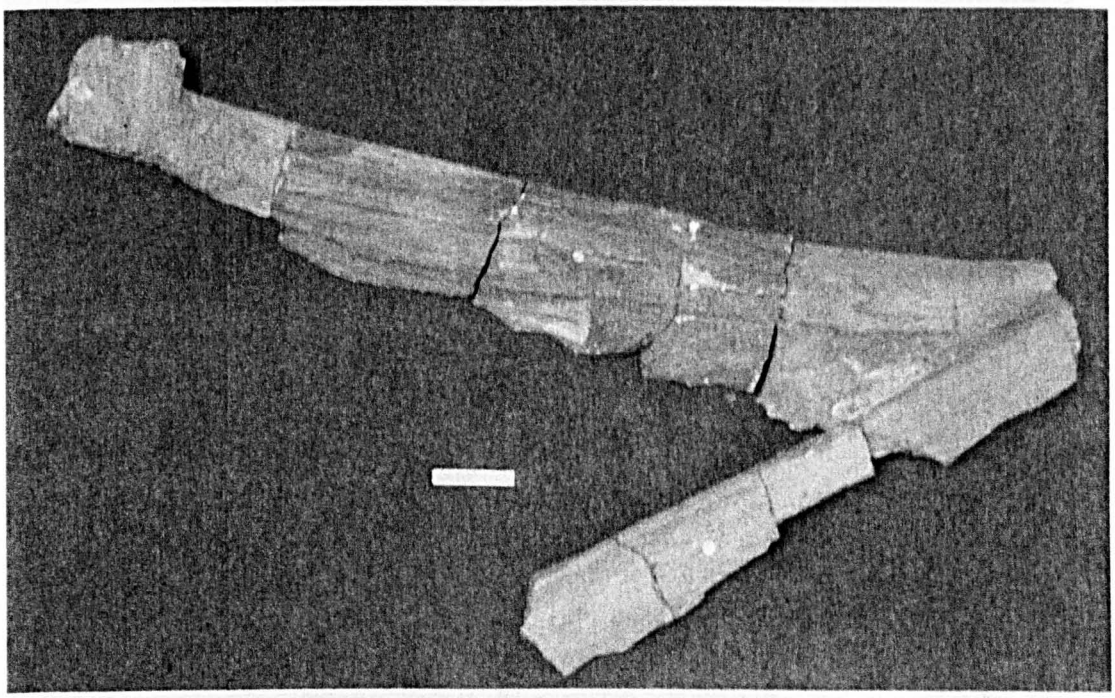


Figure 8.15. BMNH P.10156 lower element is a fragment of a 405mm left cleithrum, upper element is a 820mm long left preopercular ridge, external surface. Scale bar = 50mm.

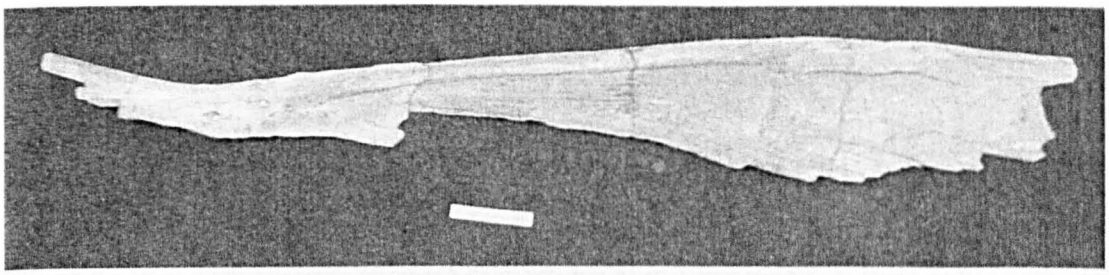


Figure 8.16a. GLAHM V3363 left maxilla, 695mm long, internal surface, rounded edge is inferior surface. Scale bar = 50mm.

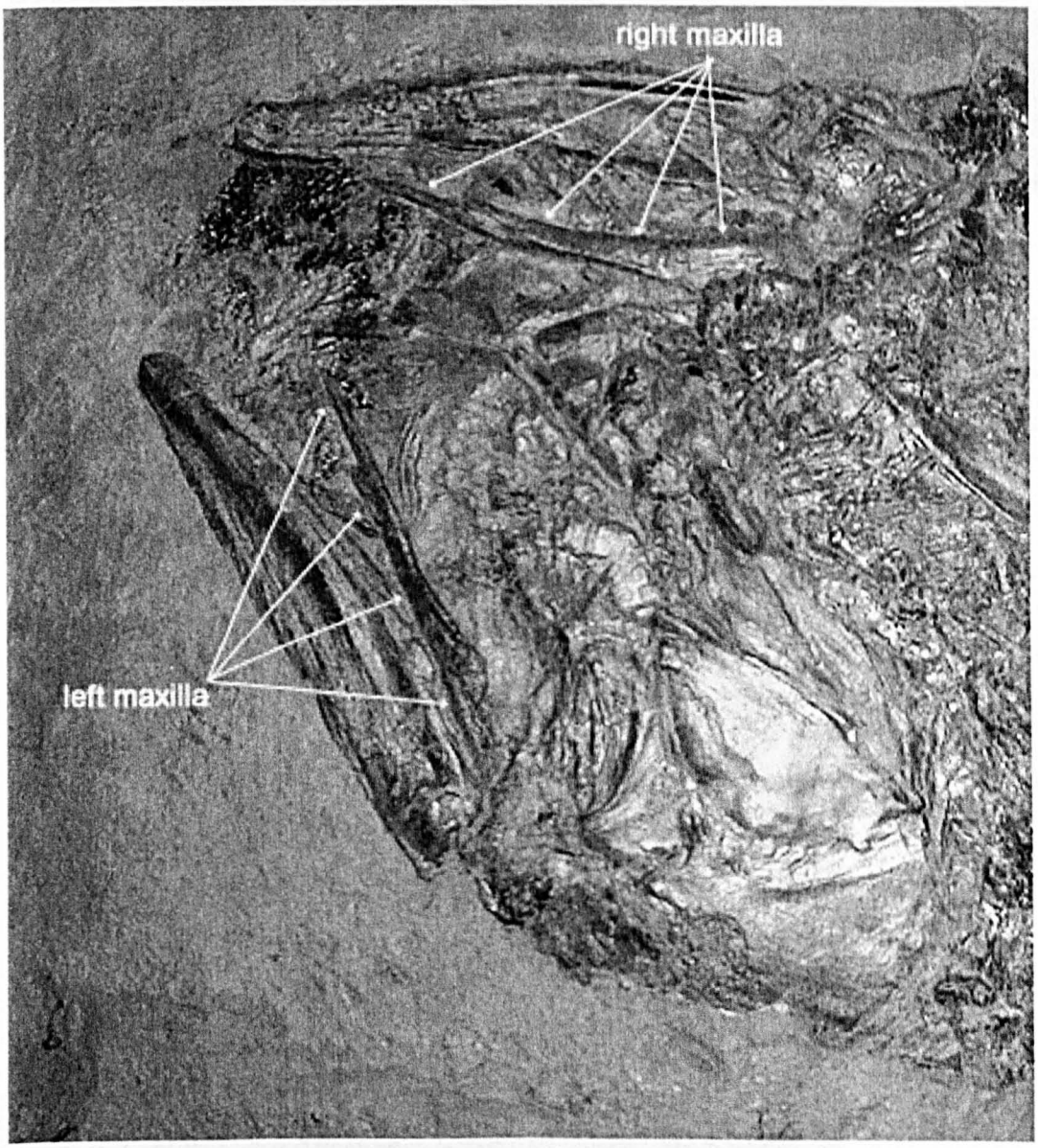


Figure 8.16b. SMNS St.52472 *Saurostomus* collapsed skull, showing left maxilla. Field of View width is 150mm.

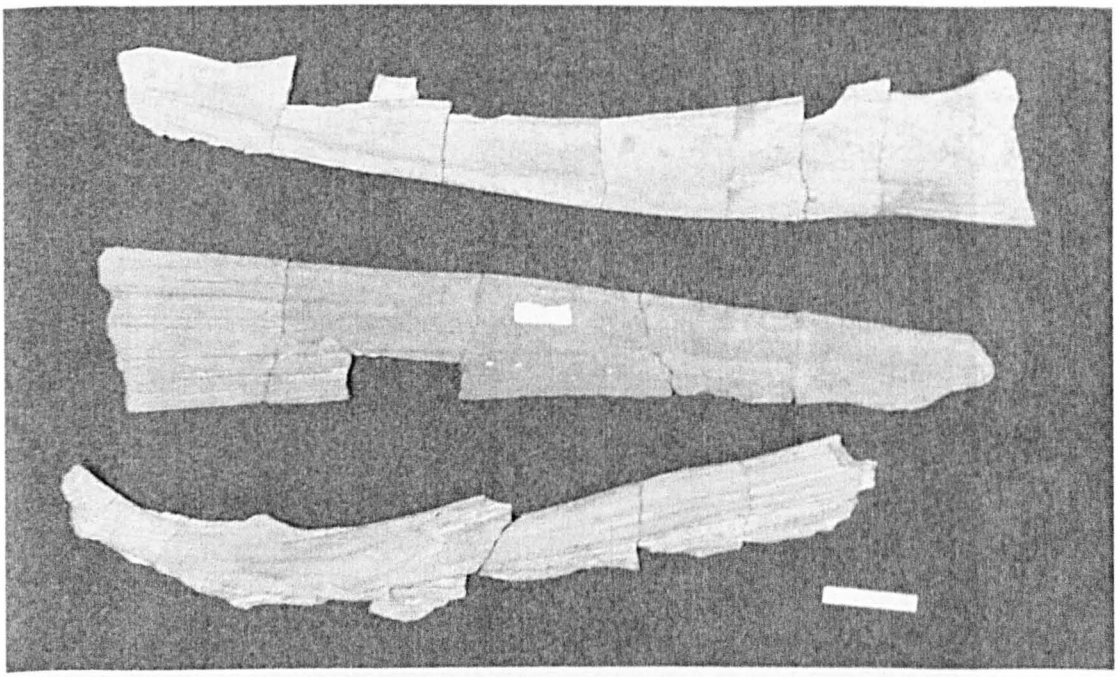


Figure 8.17. Elements similar to cleithra, but distinct. Top, GLAHM V3363 (513mm long), middle BMNH P.6921 (506mm long), bottom BMNH P.6927 (432mm long). Scale bar = 50mm.

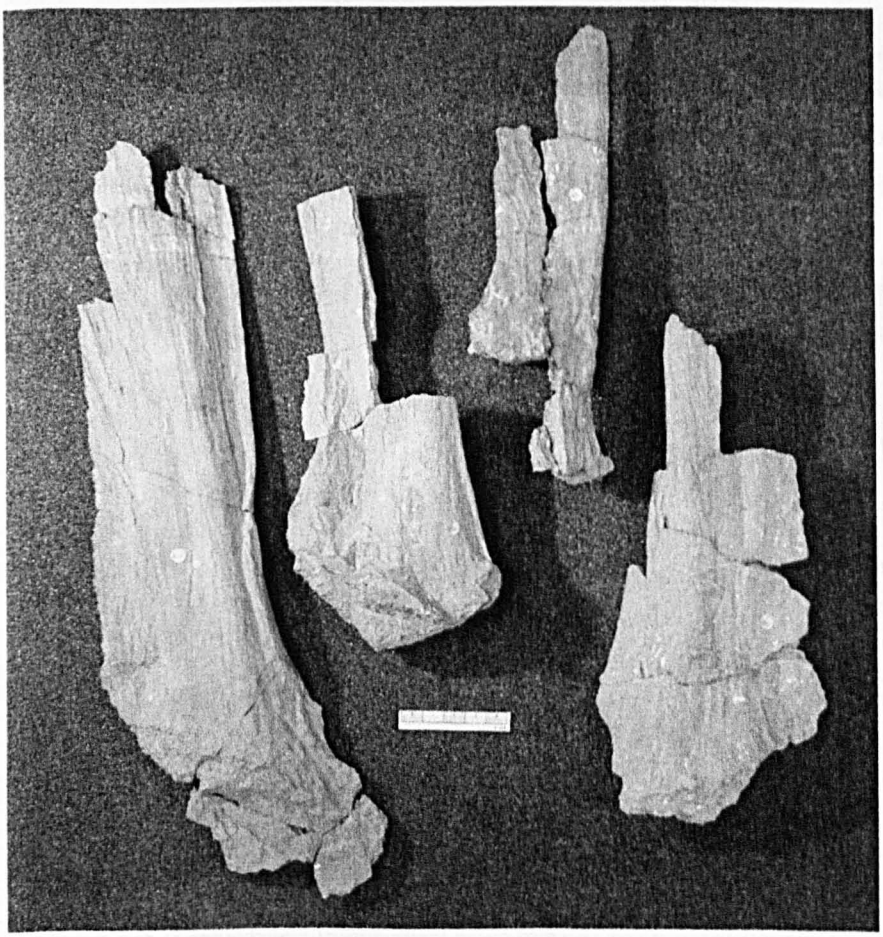


Figure 8.18. BMNH P.6921, four hypobranchials. Scale bar = 50mm.

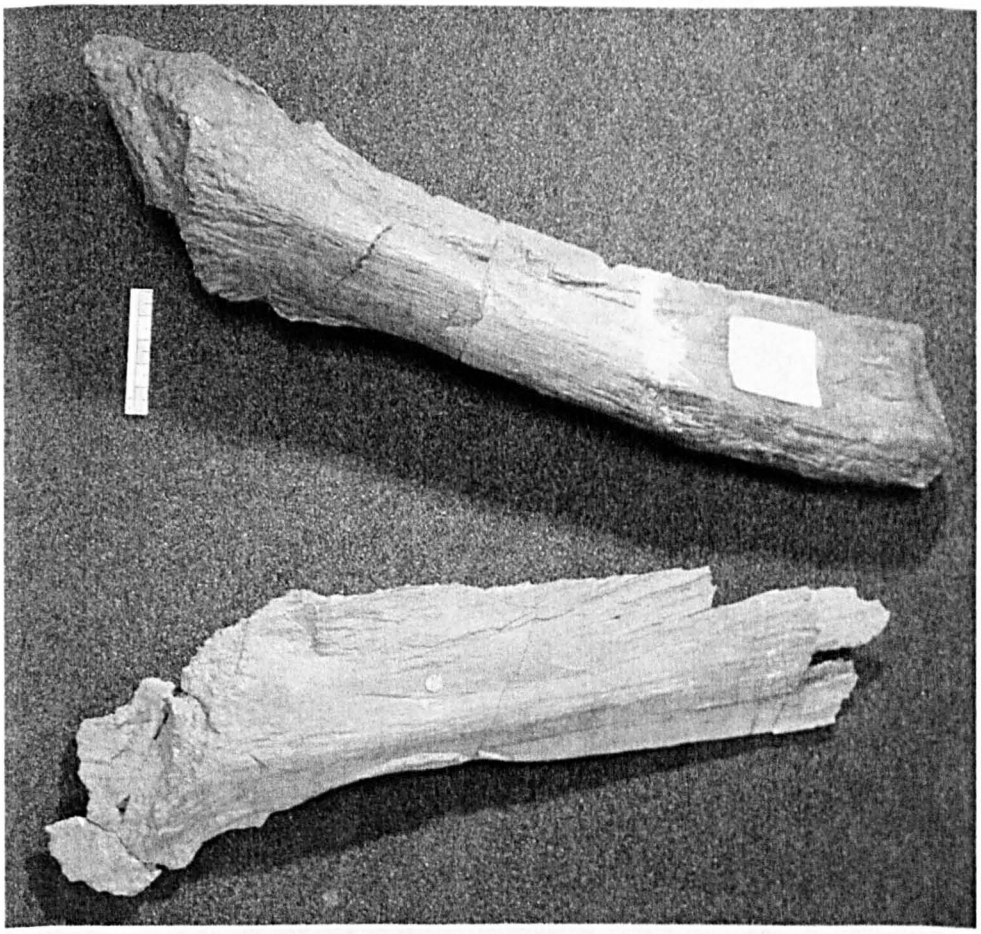


Figure 8.19. BMNH P.6921 (below) hypobranchial (368mm long) with uncrushed (above) hypobranchial from BMNH P.10156 (398mm long), external surface. Scale bar = 50mm.

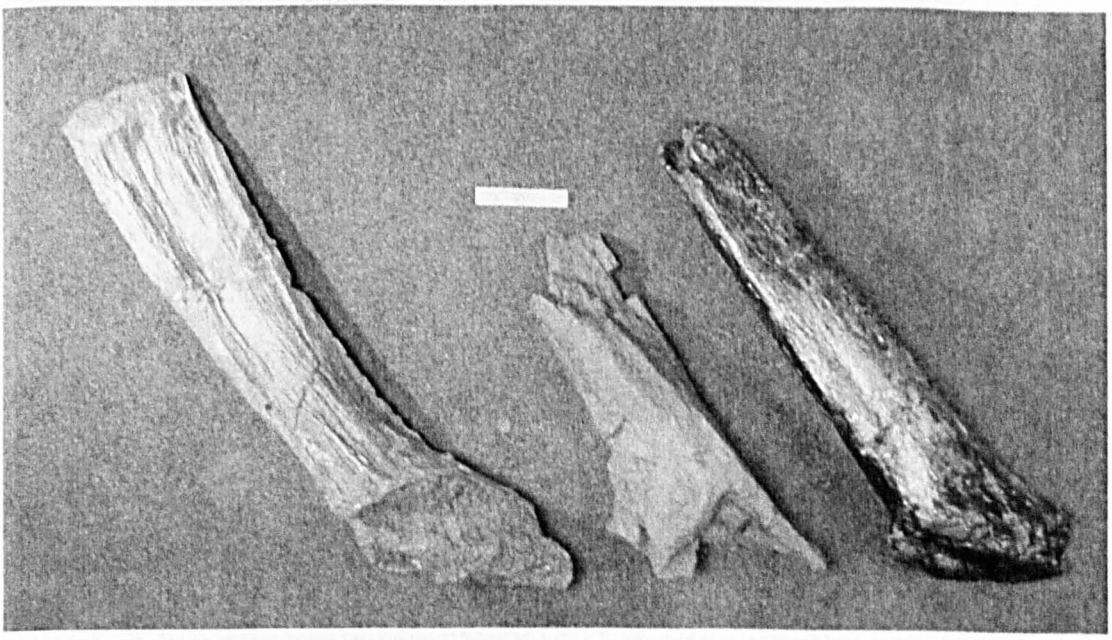


Figure 8.20a. Hypobranchial from BMNH P.10156 with cast GLAHM 109508 (of WMfN 17006/8) and stegosaur tail spine CAMSM J.46879 for comparison. Scale bar = 50mm.

Figure 8.20b. Base of stegosaur tail spine CAMSM J.46879 showing smooth articular surface. Scale bar = 50mm.

Figure 8.20c. Broken tip of stegosaur tail spine CAMSM J.46879 showing thick uncrushed bone surrounding a cavity. Scale bar = 50mm.

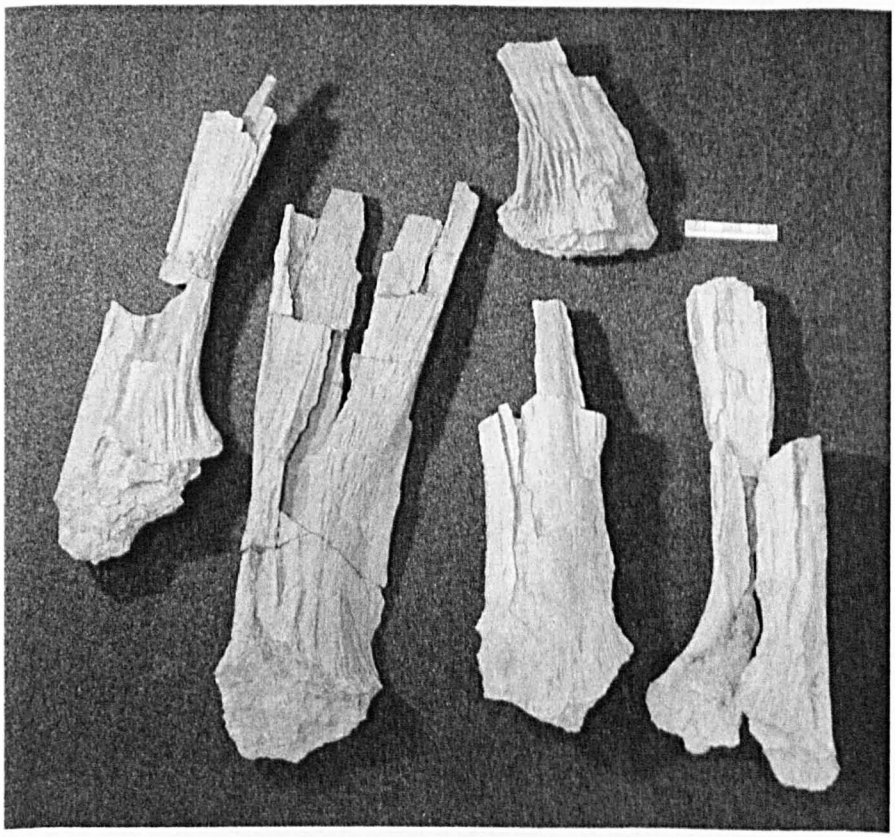


Figure 8.21. Hypobranchials from GLAHM V3363. Scale bar = 50mm.

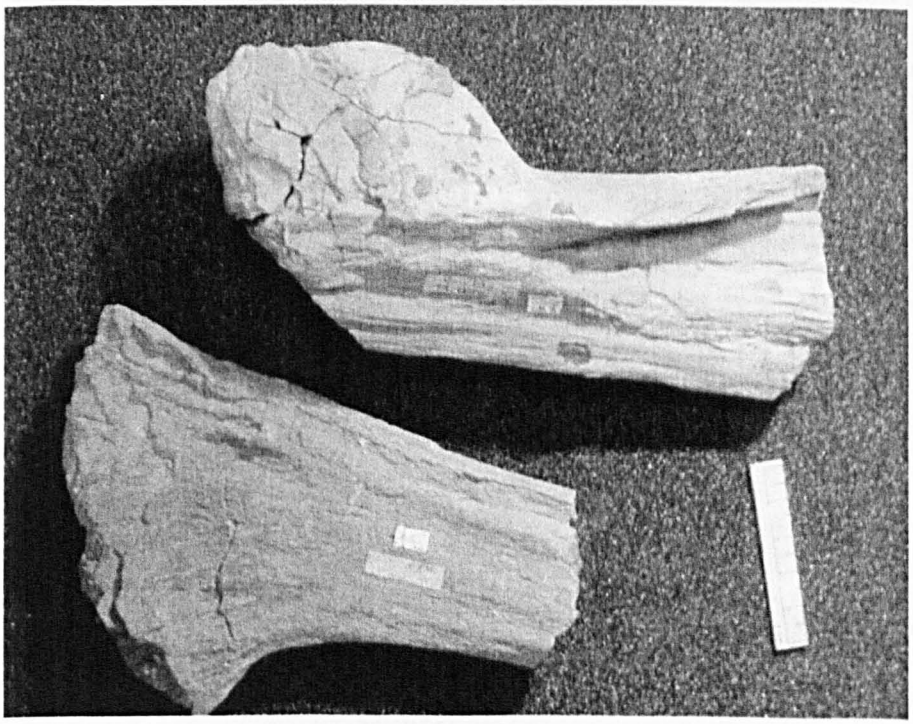


Figure 8.22. Hypobranchials from CAMSM X.50115 (top) and CAMSM X.50118 (bottom). Scale bar = 50mm.

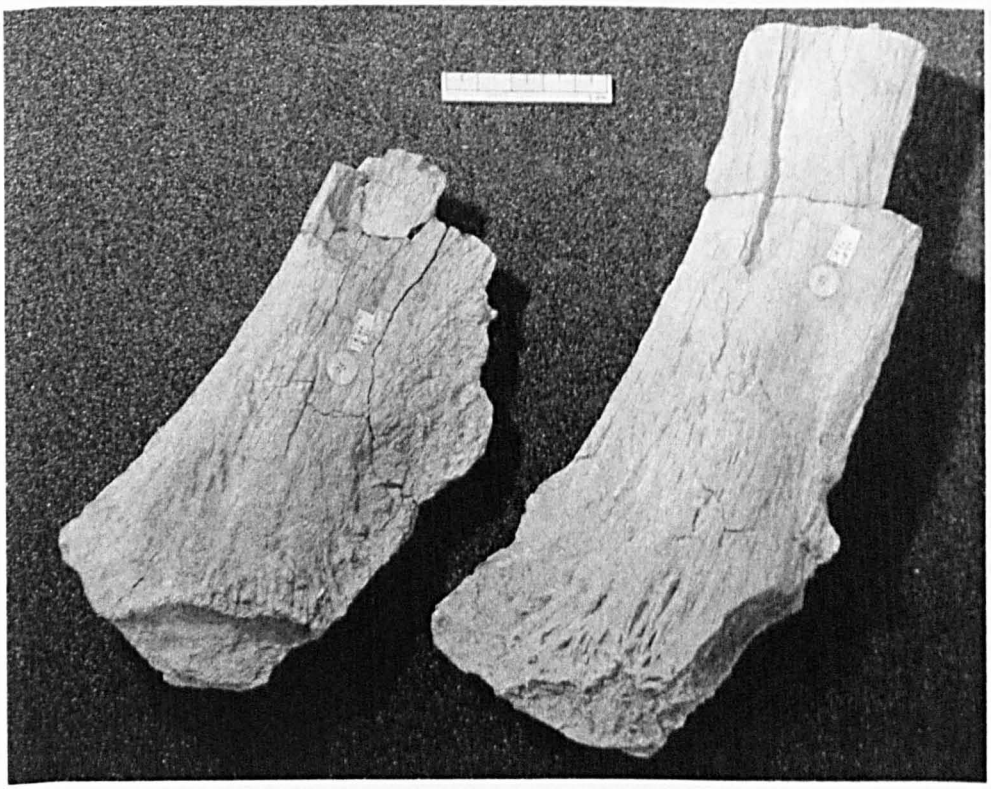


Figure 8.23. Hypobranchials NMW 19.96.G8/33 and NMW 19.96.G8/34. Scale bar = 50mm.

Figure 8.24. Hypobranchial LEICT G418.1956.15.5 (left) and LEICT G418.1956.15.2 (right). Scale bar = 50mm.

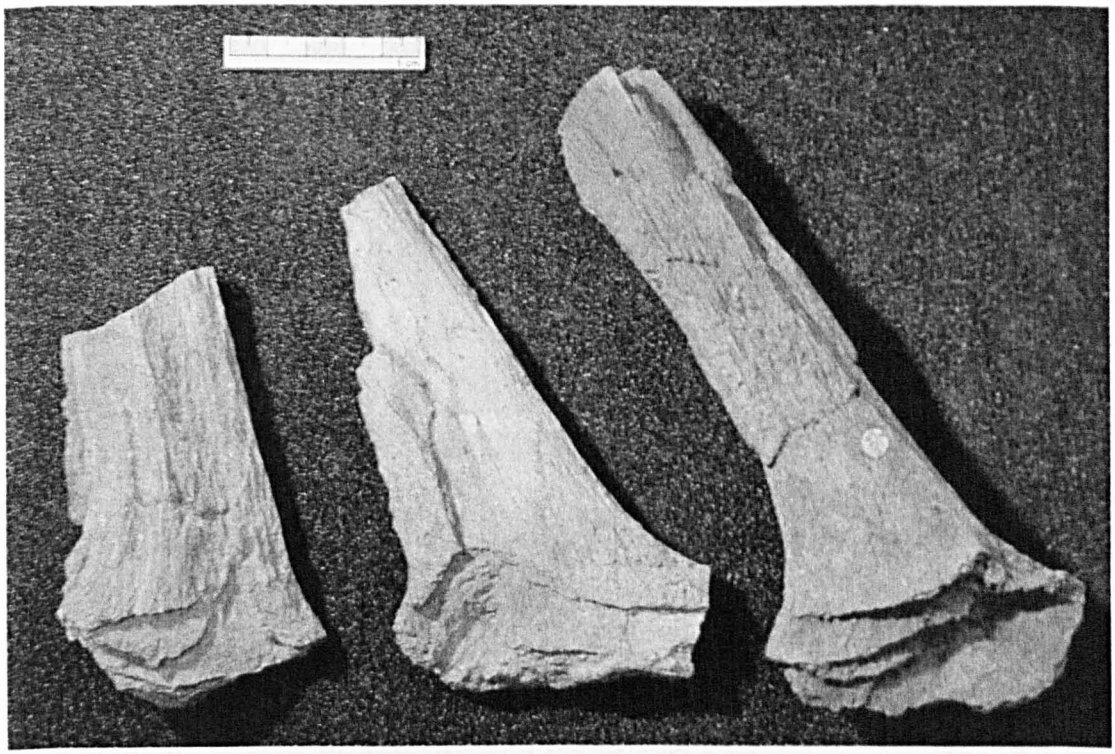


Figure 8.25. Hypobranchials from BMNH P.11823. Scale bar = 50mm.

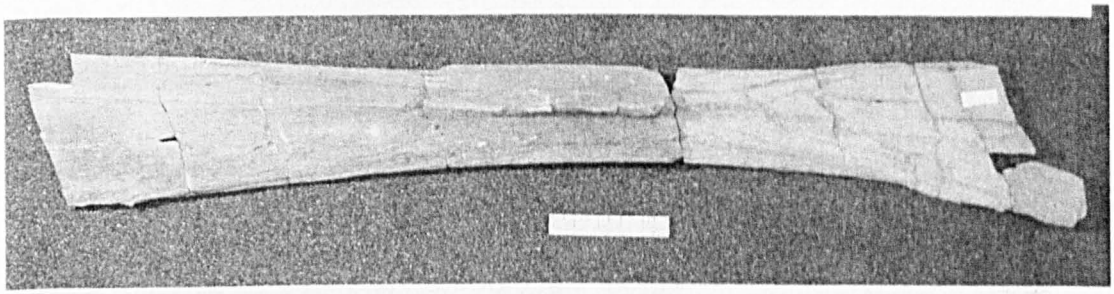


Figure 8.26. Ceratobranchial III from BMNH P.11823. Scale bar = 50mm.

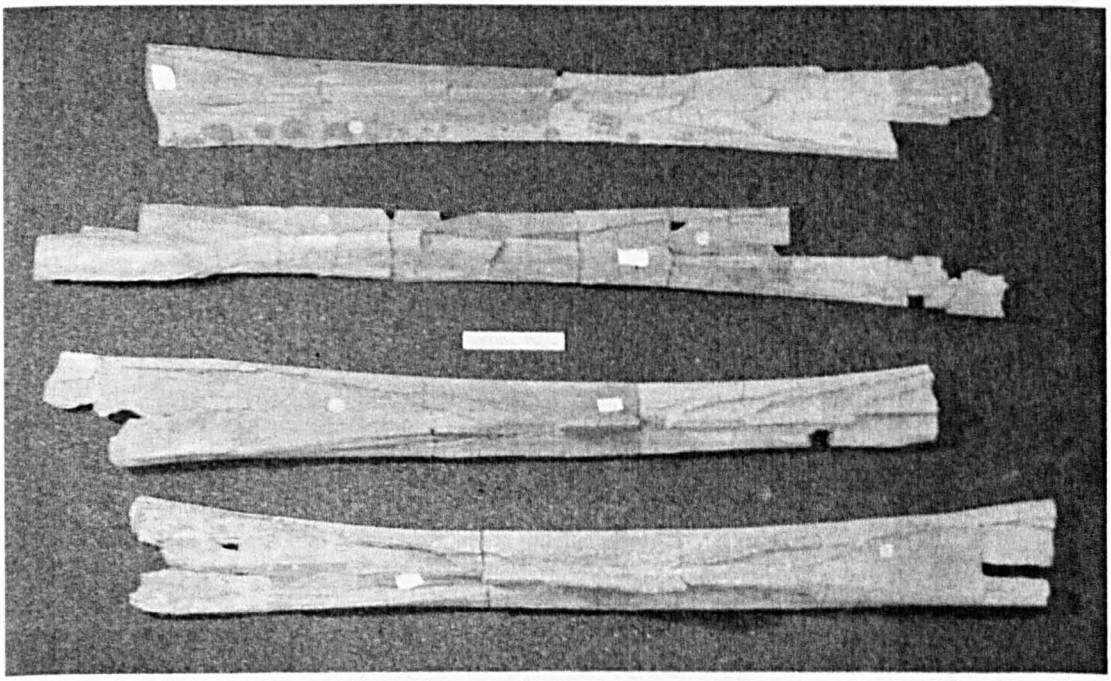


Figure 8.27. Ceratobranchials II+IV from BMNH P.11823. Scale bar = 50mm.

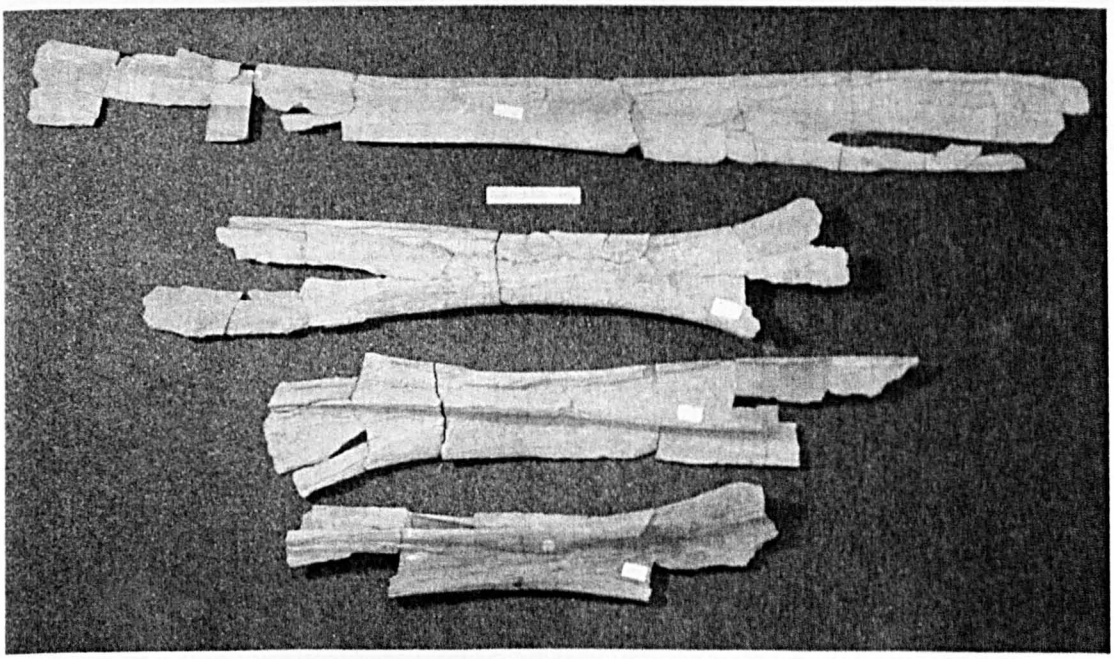


Figure 8.28. Ceratobranchial I (top) with three epibranchials from BMNH P.11823. Scale bar = 50mm.

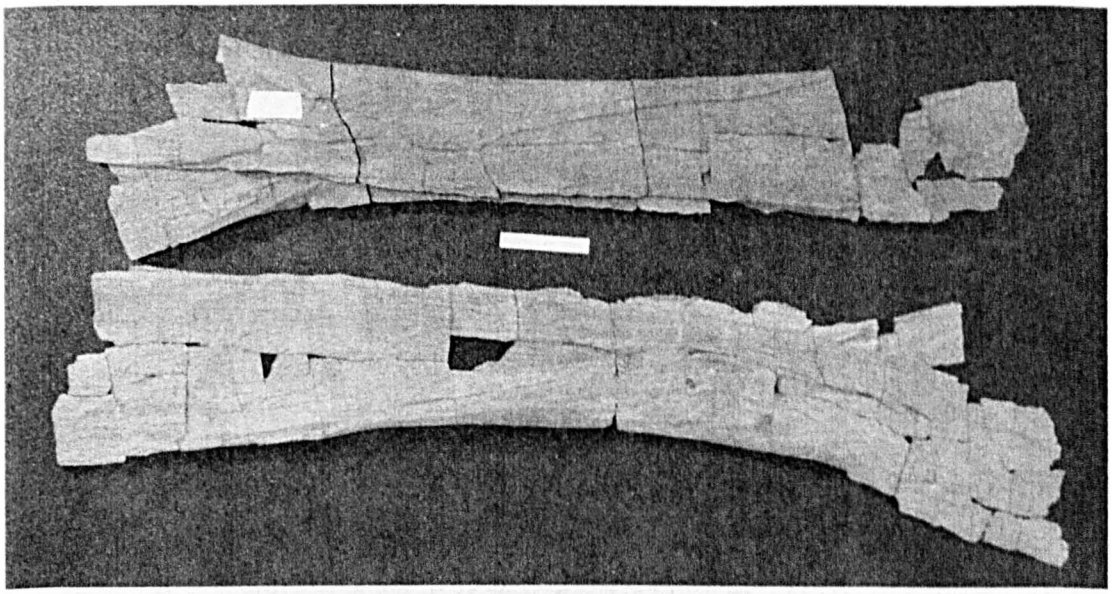


Figure 8.29. Both epibranchial Is from BMNH P.10000. Scale bar = 50mm.

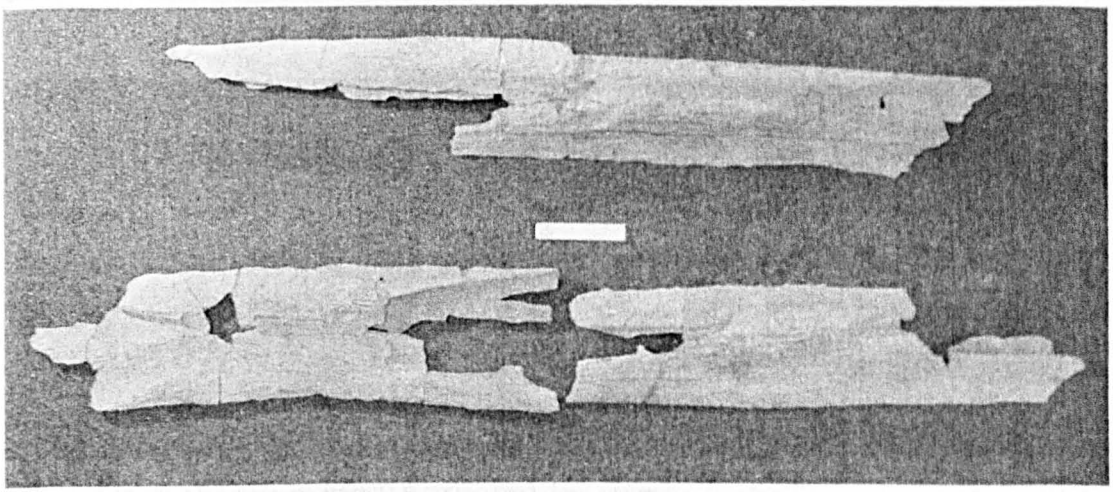


Figure 8.30. Three ceratobranchial fragments from BMNH P.10000. Scale bar = 50mm.

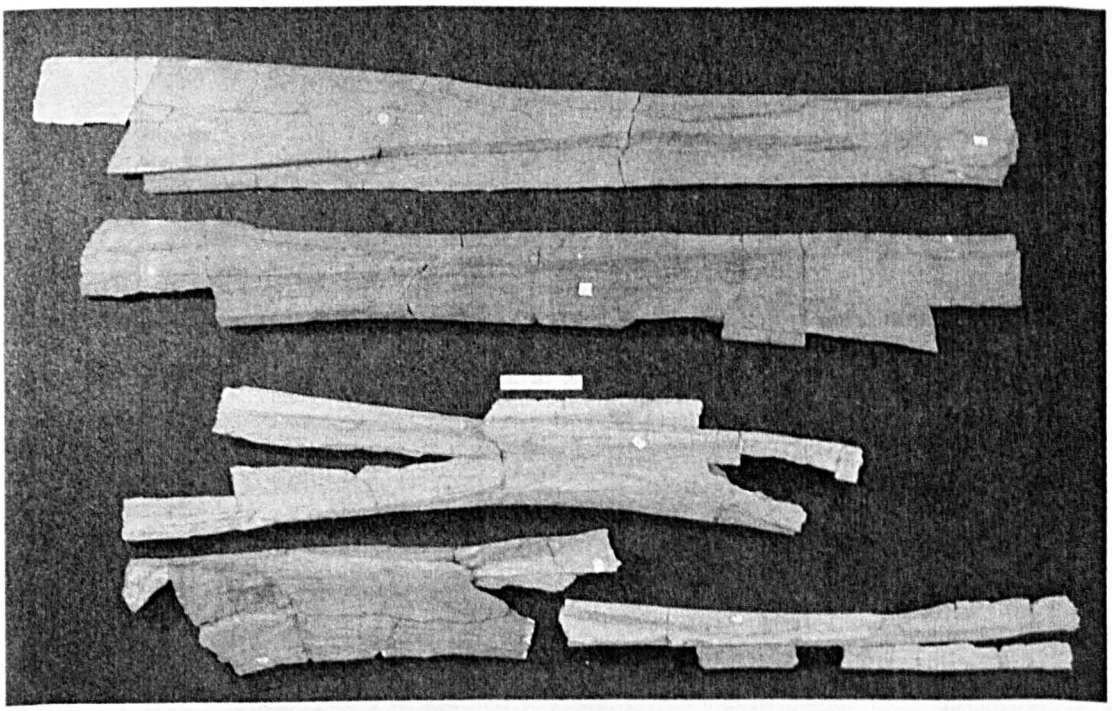


Figure 8.31. The five branchial arch elements from BMNH P.6921. Scale bar = 50mm.

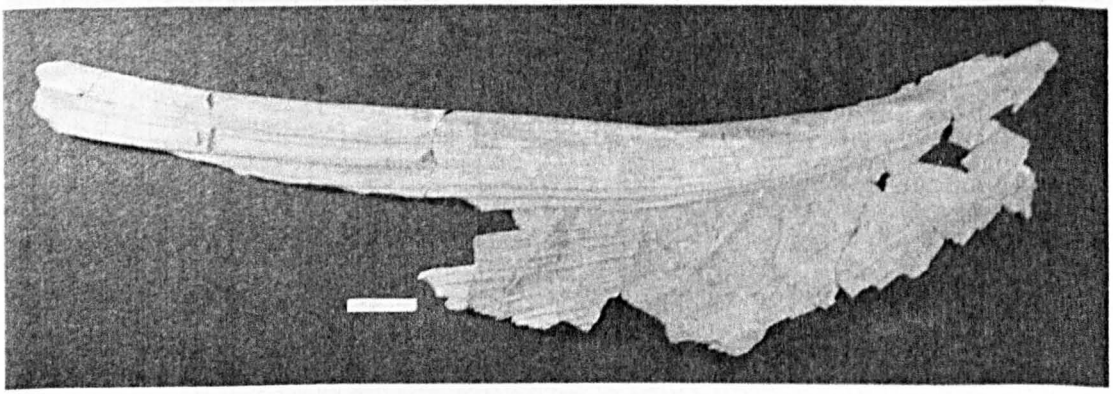


Figure 8.32. Right preopercle BMNH P.6922. Scale bar = 50mm.

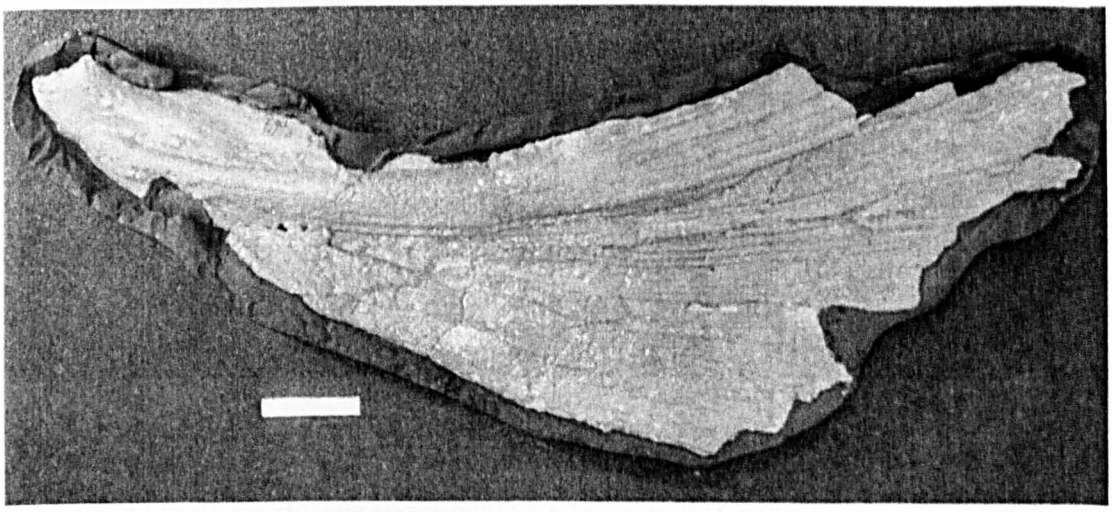


Figure 8.33. Left preopercle PETMG F.174/182. Scale bar = 50mm.

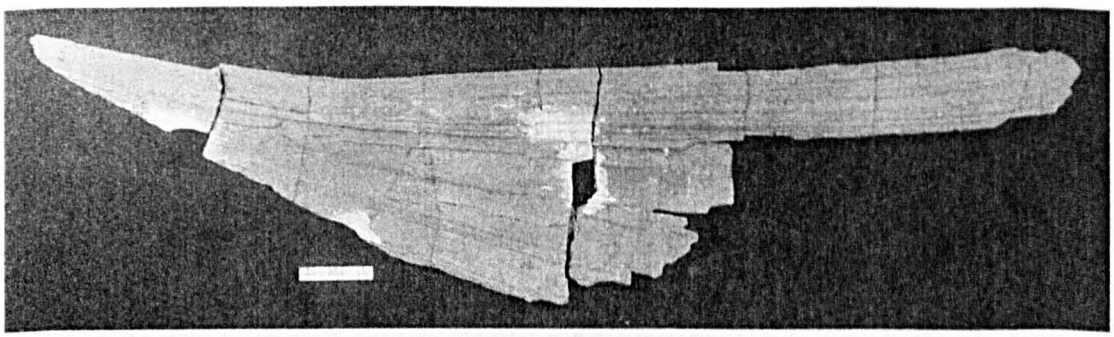


Figure 8.34. Left ?preopercle GLAHM V3363. Scale bar = 50mm.

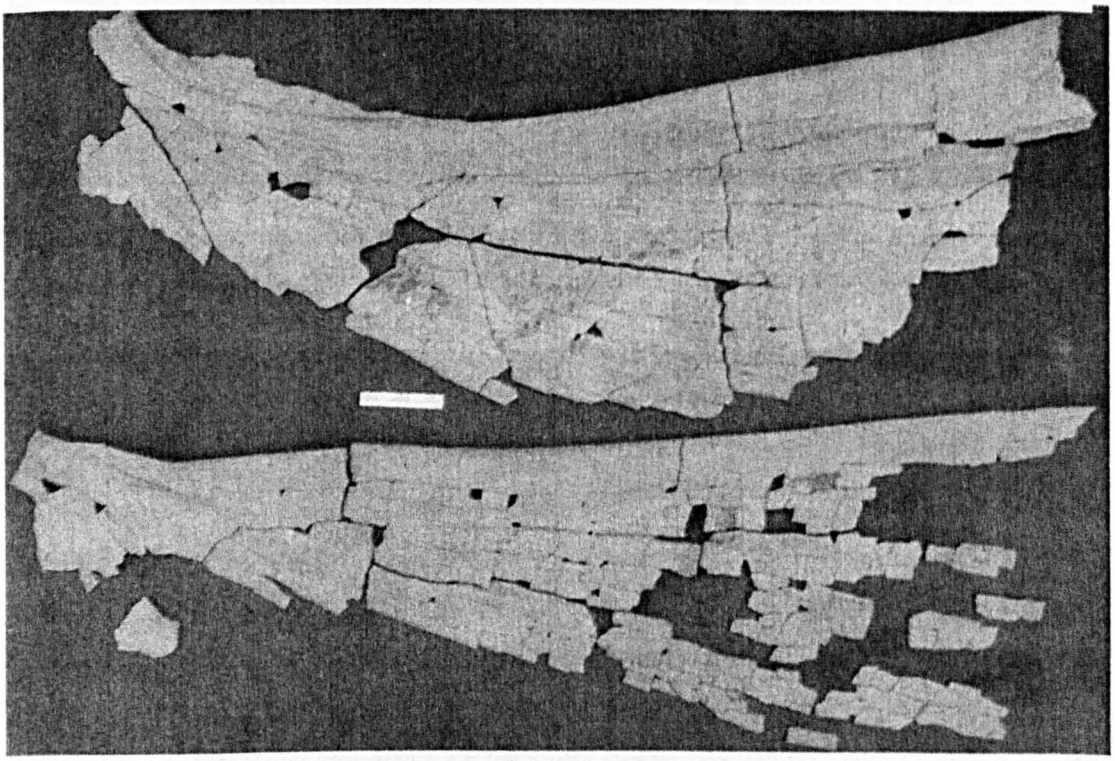


Figure 8.35. Preopercle-like bones from BMNH P.10000. Scale bar = 50mm.

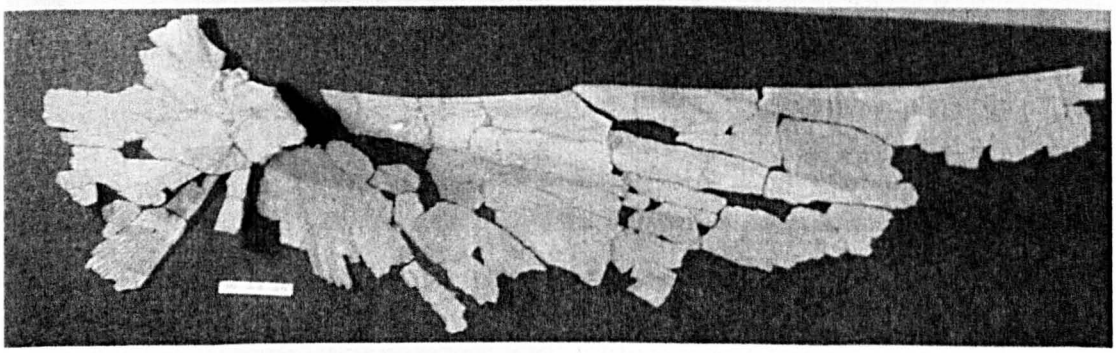


Figure 8.36. 'Butterfly' bone from GLAHM V3363. Scale bar = 50mm.

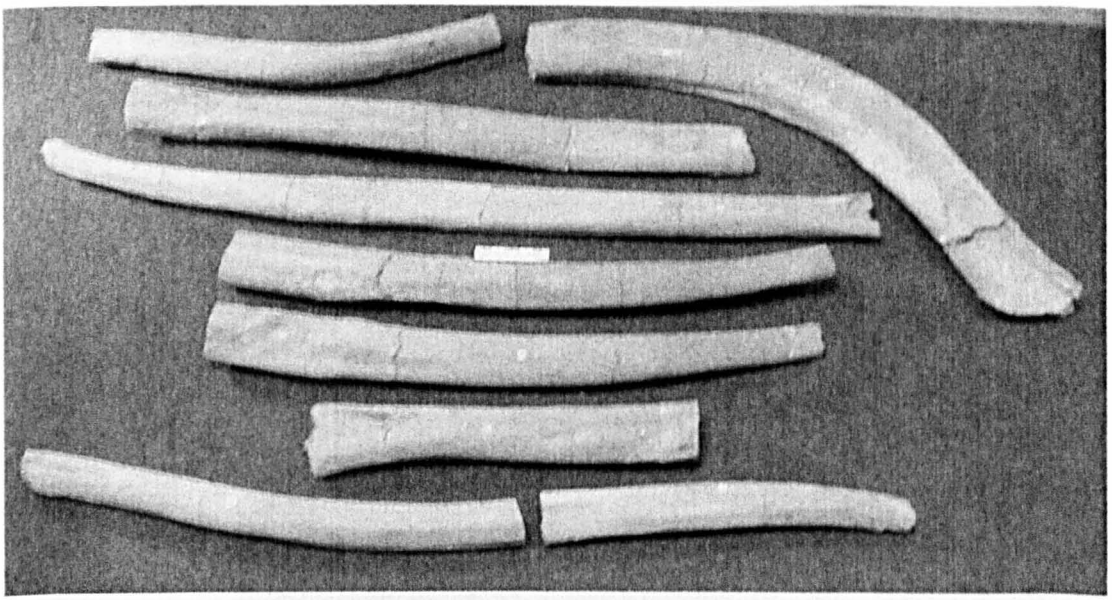


Figure 8.37. The nine 'rib-shaped' bones of BMNH P.6921 marked as being used for Smith Woodward's identification. The longest and most complete example sits above the scale bar. Scale bar = 50mm.

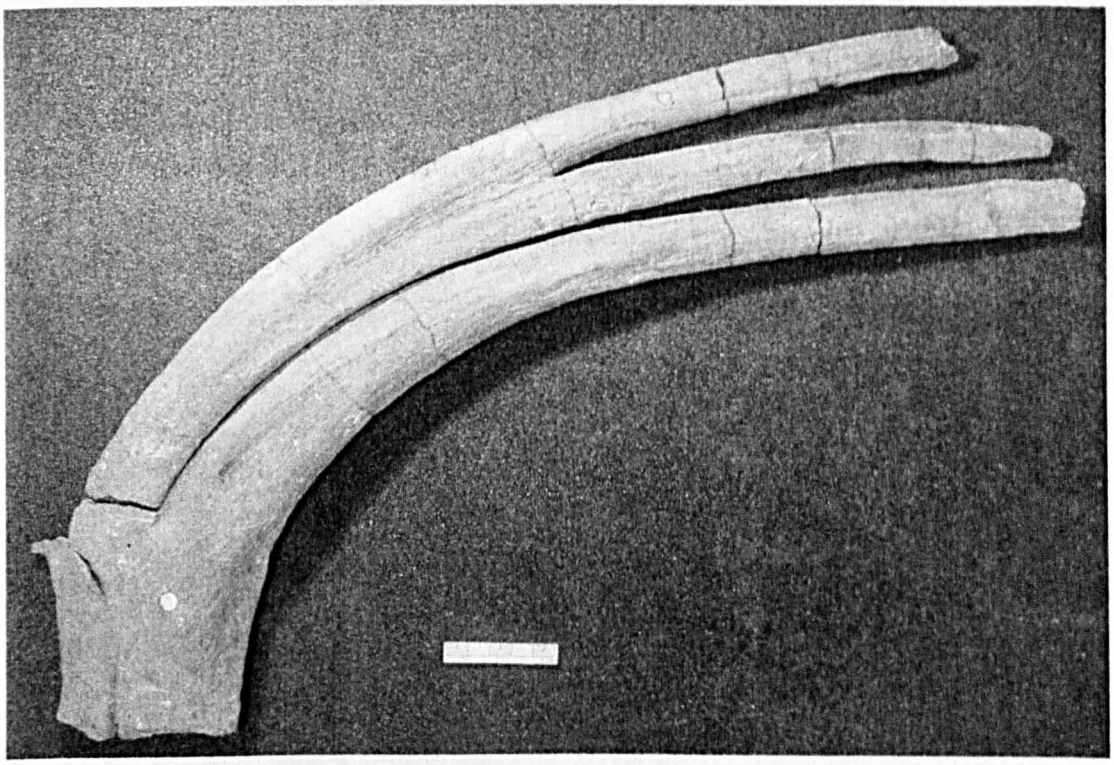


Figure 8.38. Three-way branching in BMNH P.11826. Scale bar = 50mm.

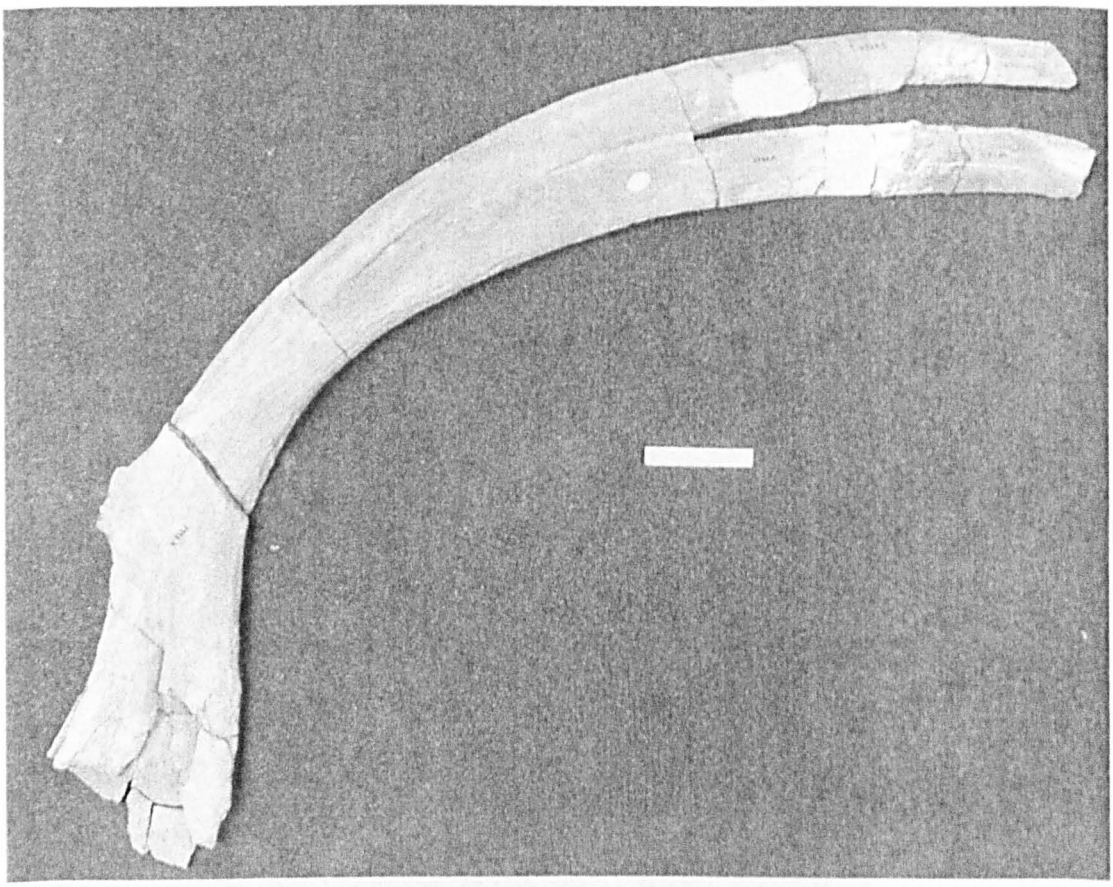


Figure 8.39a. Two-way branching in GLAHM V3363. Scale bar = 50mm.

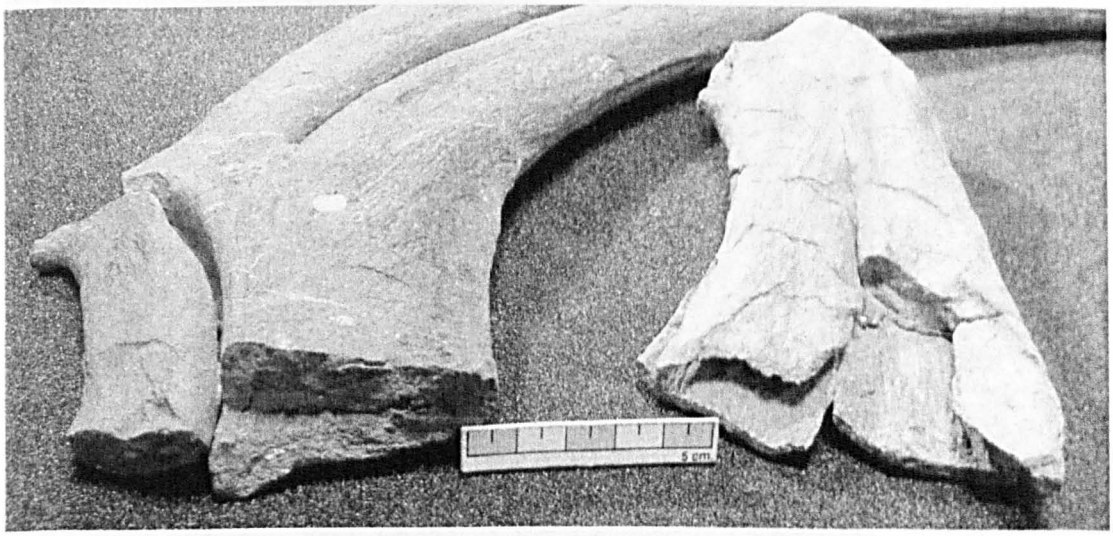


Figure 8.39b. Comparison between thickness of bone at base of GLAHM V3363 and BMNH P.11826. Scale bar = 50mm.

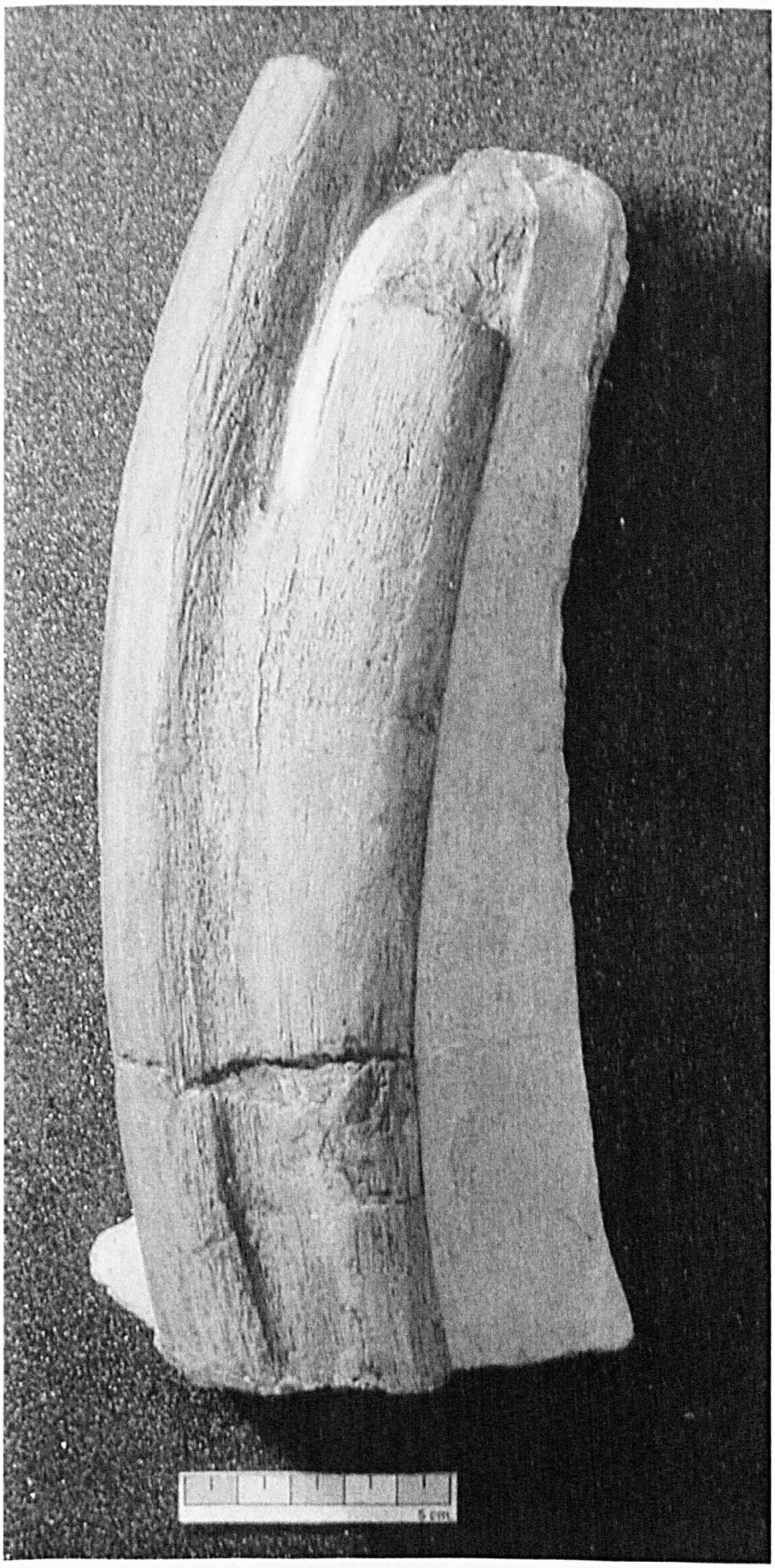


Figure 8.40a. Medio-lateral and dorso-ventral branching in cast GLAHM 109441, side view. Scale bar = 50mm.

Figure 8.40b. Medio-lateral and dorso-ventral branching in cast GLAHM 109441, skewed plan view. Scale bar = 50mm.

Figure 8.40c. Part of dorsal fin of JM SOS 3556 *Asthenocormus*, showing two fully divided layers of left and right hemitrichia.

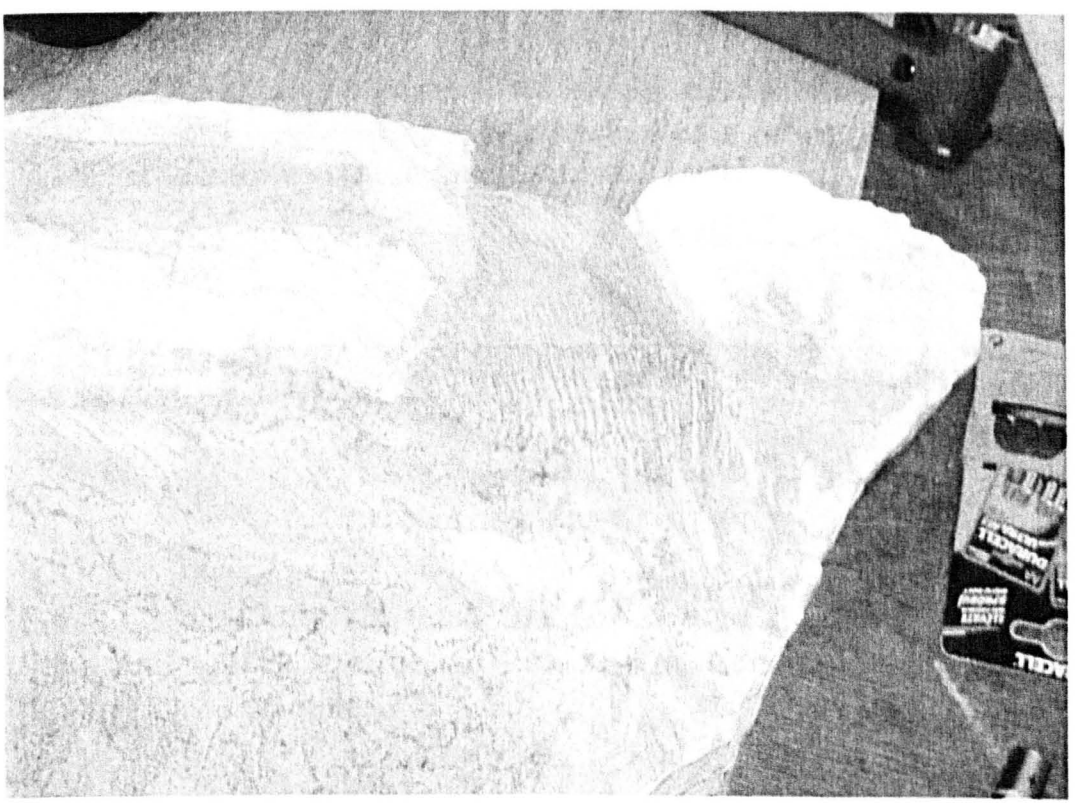


Figure 8.40d. Counterpart of dorsal fin of JM SOS 3556 *Asthenocormus*, showing two fully divided layers of left and right hemitrichia.

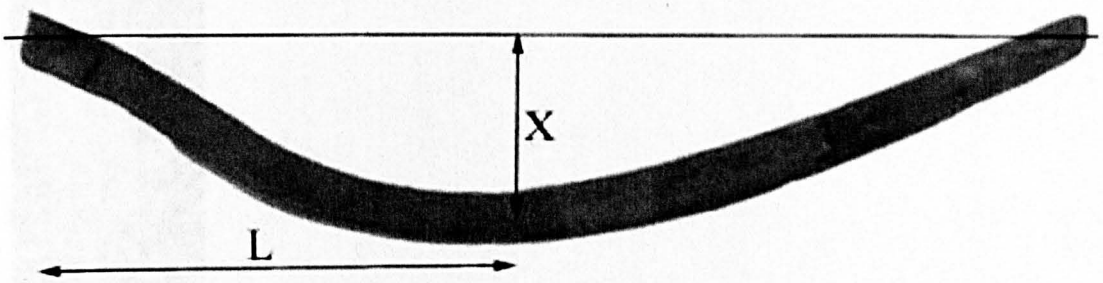


Figure 8.41a. Diagram (after Biewener 1983b) showing measurements taken for curvature analysis.

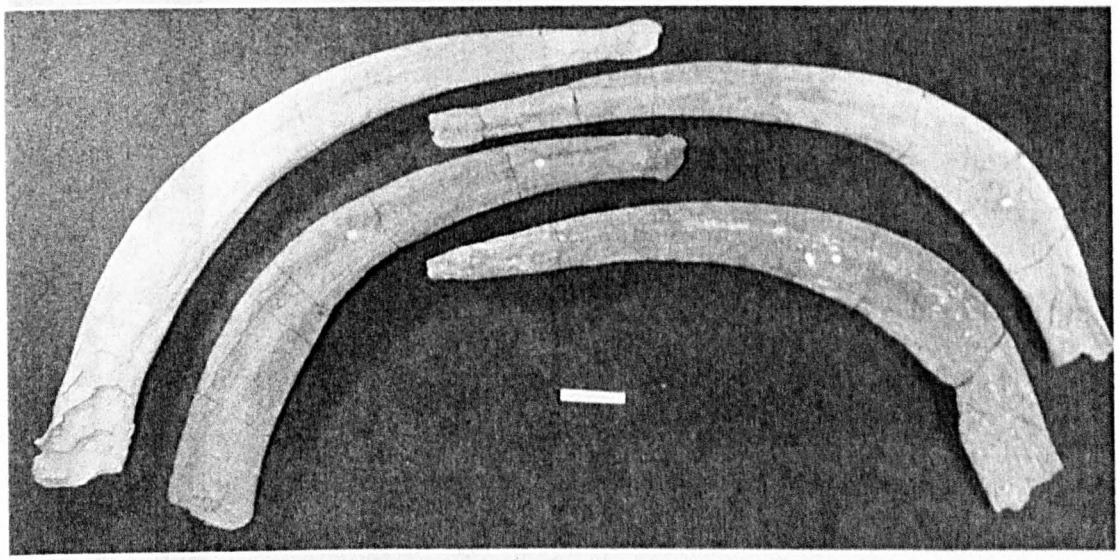


Figure 8.41b. Robust curved elements assessed for curvature as indicator of relative mass, lateral view. From left to right NMW 19.96.G9/2, BMNH P.11825, BMNH P.6925, GLAHM V3363. Scale bar = 50mm.

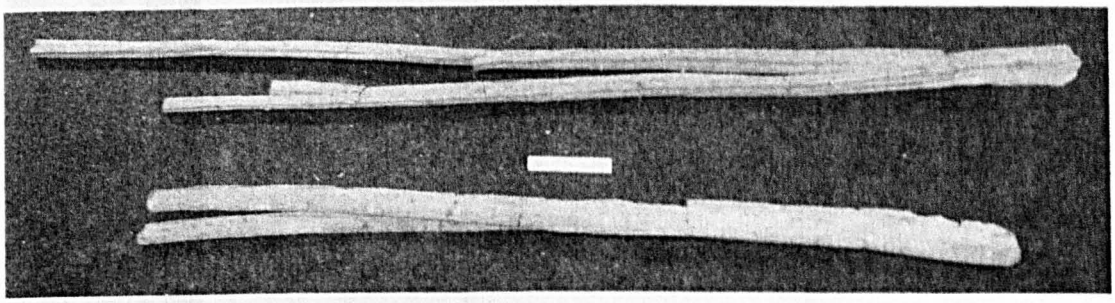


Figure 8.42a. Caudal (top, 697mm long) and pectoral fin-ray fragments (bottom, 568mm long) from BMNH P.6921. Scale bar = 50mm.

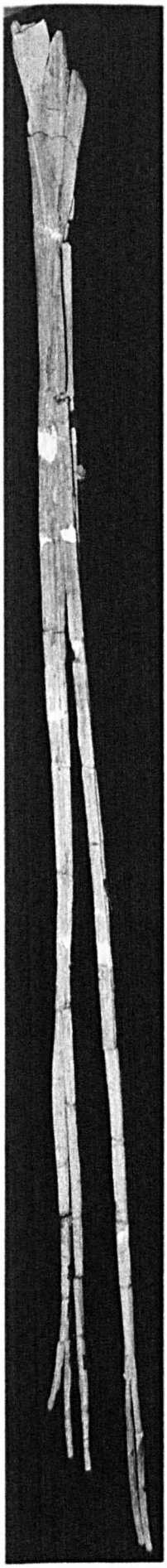


Figure 8.42b. Caudal fin-ray (1225mm long) GLAHM V3362.

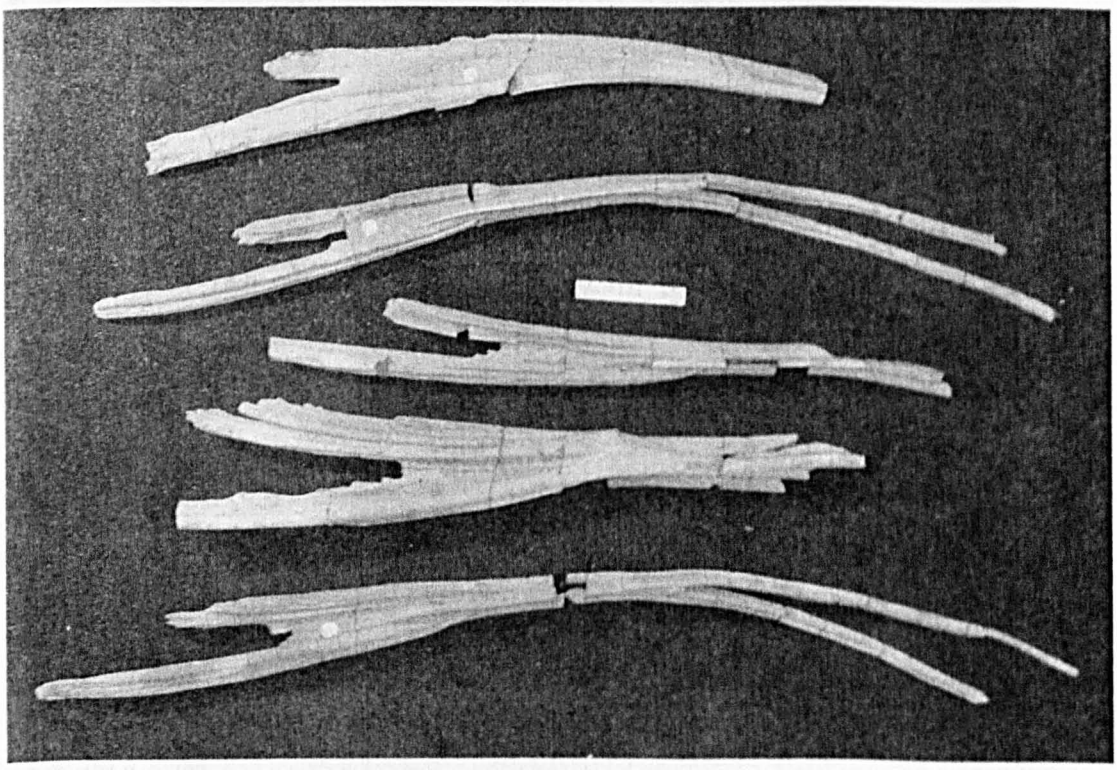


Figure 8.42c. Distal actinotrichia from the pectoral fins of BMNH P.6921. Scale bar = 50mm.

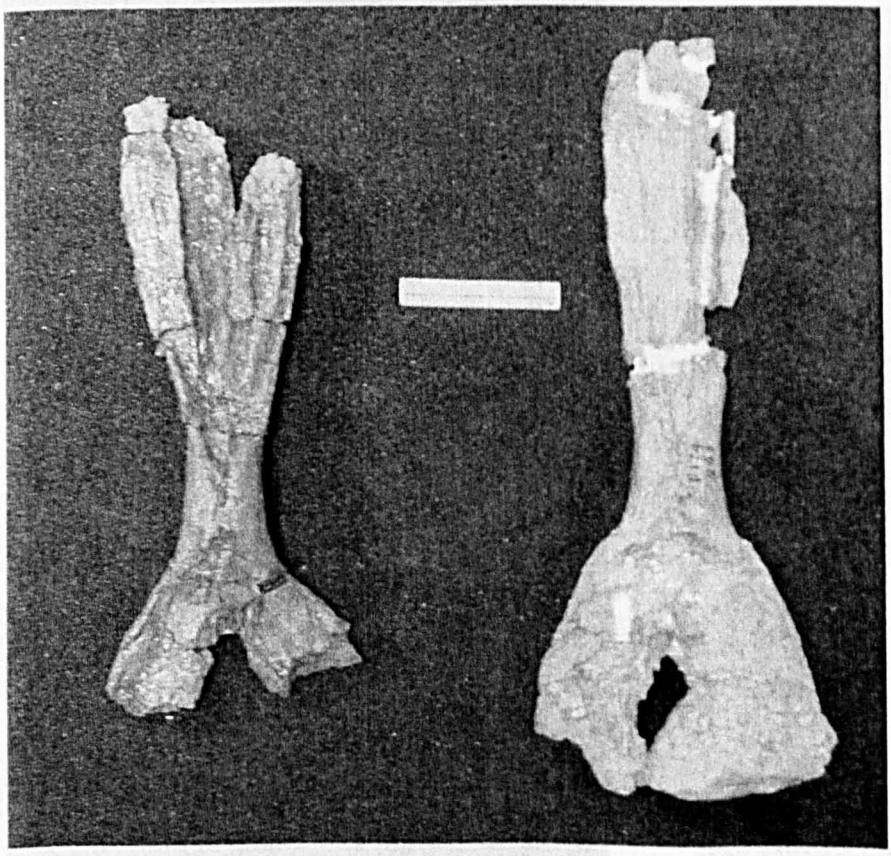


Figure 8.43. Radiale I (left, 199mm long, PETMG F.174/245) and radiale II (right, 250mm long, PETMG F.174/263) from the right pectoral fin. Scale bar = 50mm.

Figure 8.44. Radiale II (left, 118mm long) and radiale I (right, 101mm long) from BMNH P.6921. Scale bar = 50mm.

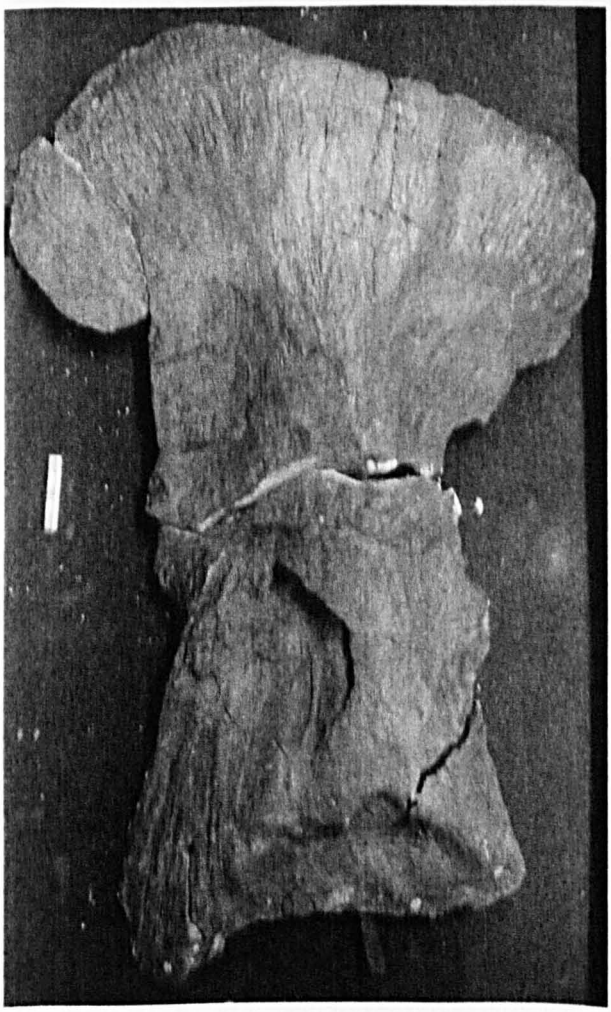


Figure 8.45a. Left hyomandibula from BMNH P.10156, 687mm long. Scale bar = 50mm.

Figure 8.45b. Left hyomandibula from *Saurostomus* specimen from Holzmaden. Height = 15mm.

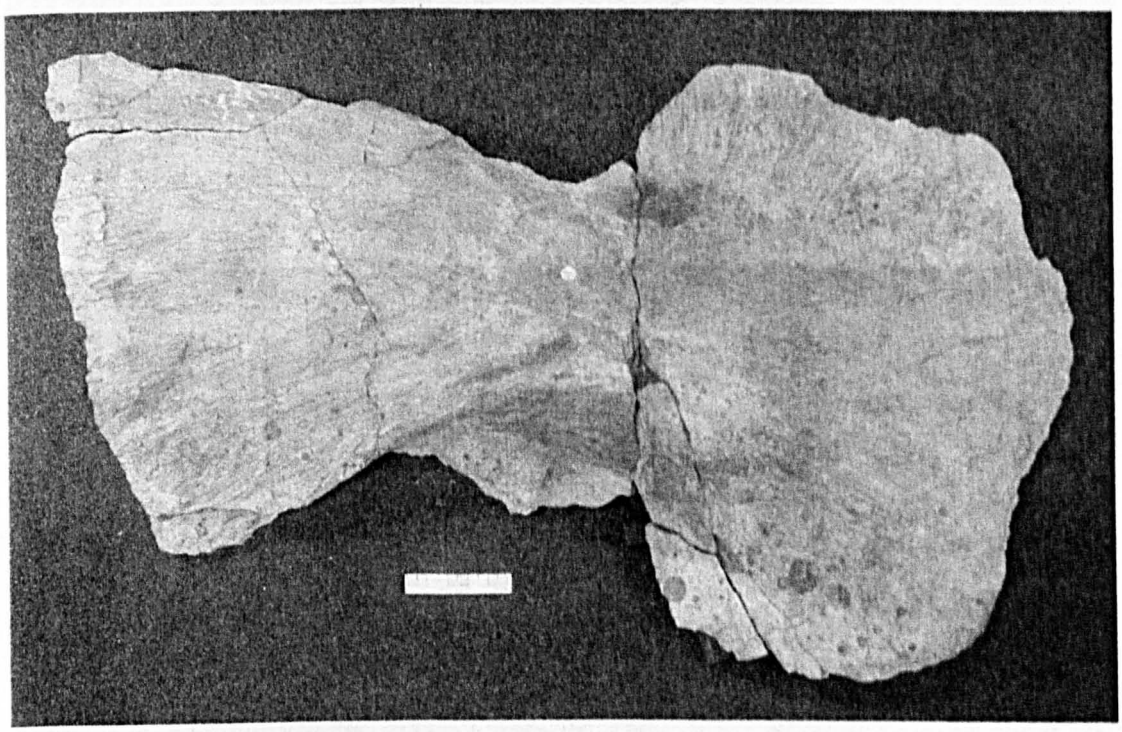


Figure 8.46a. Left hyomandibula from BMNH P.11823, 557mm long. Scale bar = 50mm.

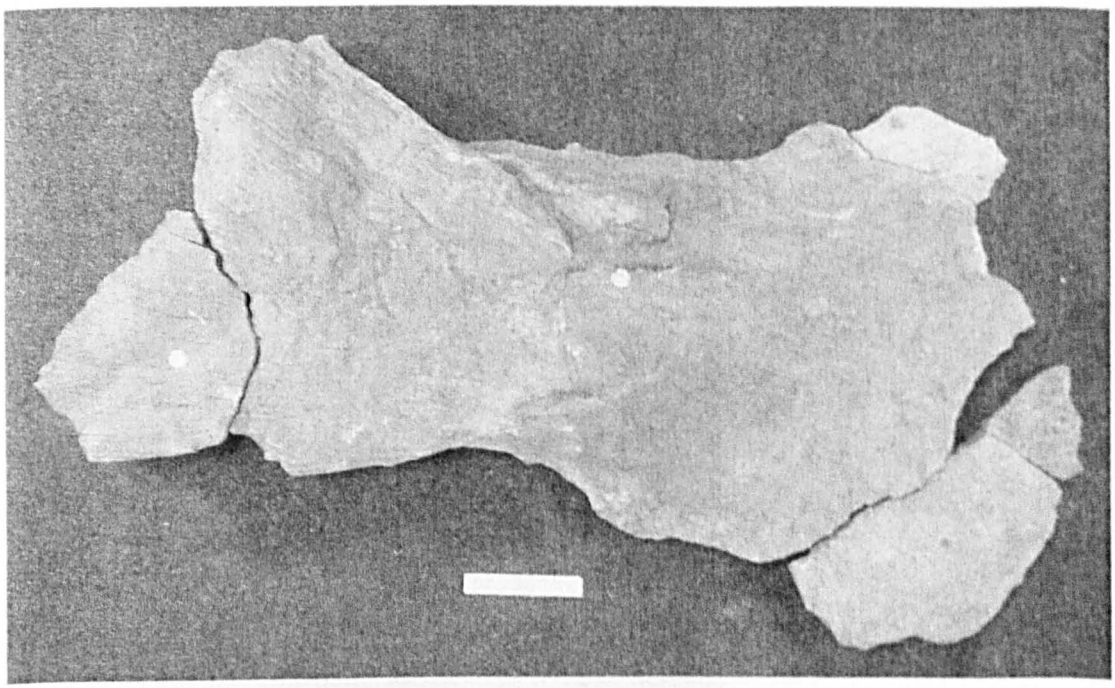


Figure 8.46b. Right hyomandibula from BMNH P.11823, 487mm long. Scale bar = 50mm.

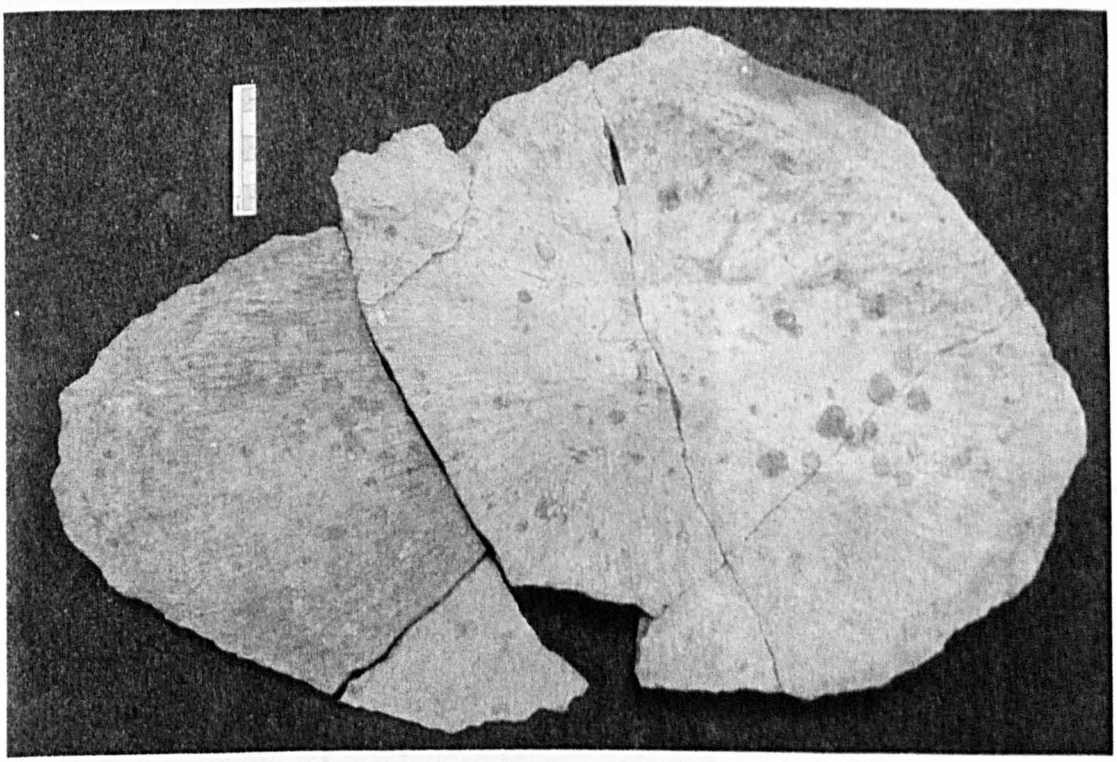


Figure 8.47. Possible left subopercle from BMNH P.11823. Scale bar = 50mm.

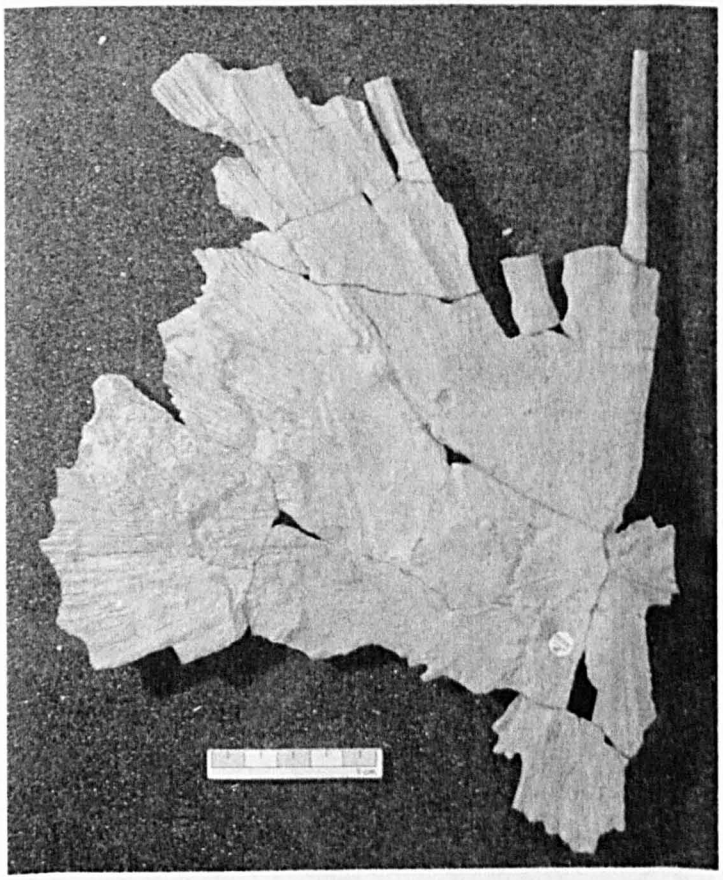


Figure 8.48a. Unknown bone from BMNH P.11826. Scale bar = 50mm.

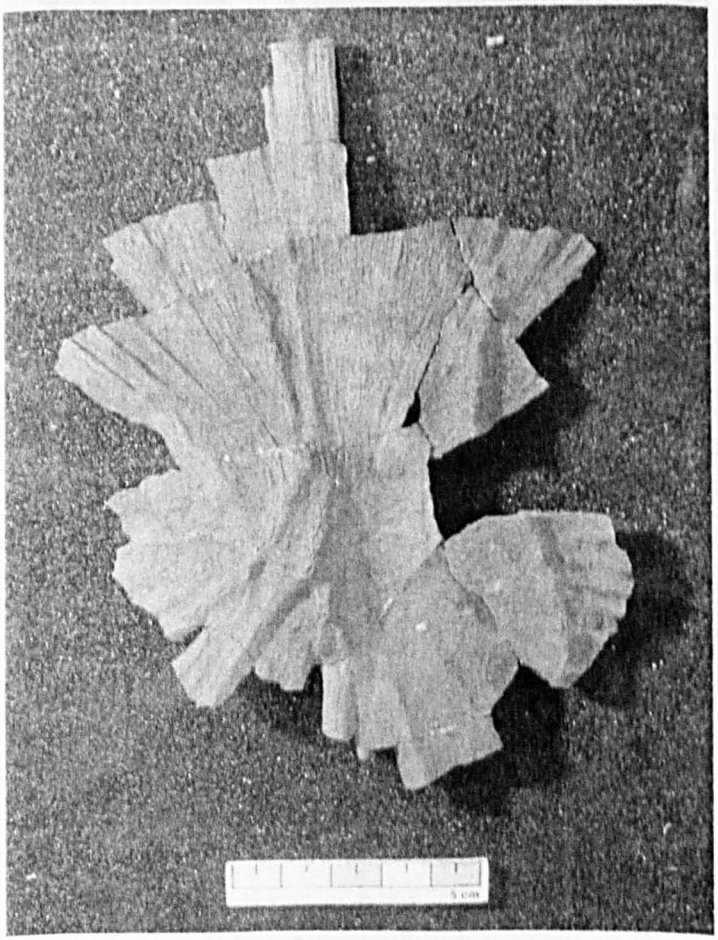


Figure 8.48b. Unknown bone from BMNH P.11823. Scale bar = 50mm.

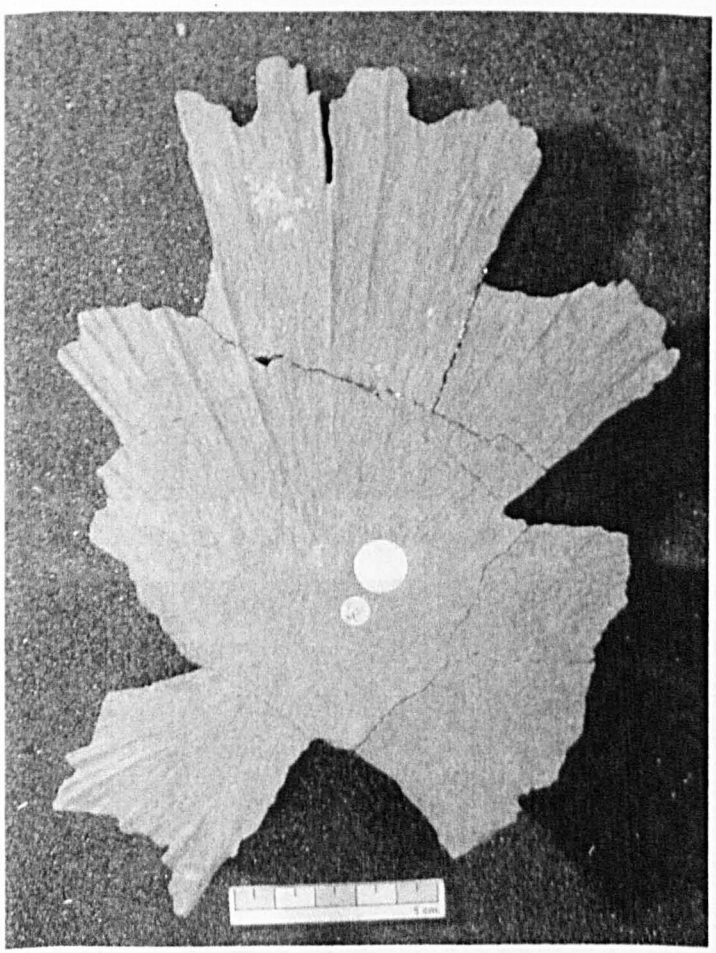


Figure 8.48c. Unknown bone from BMNH P. 6921. Scale bar = 50mm.

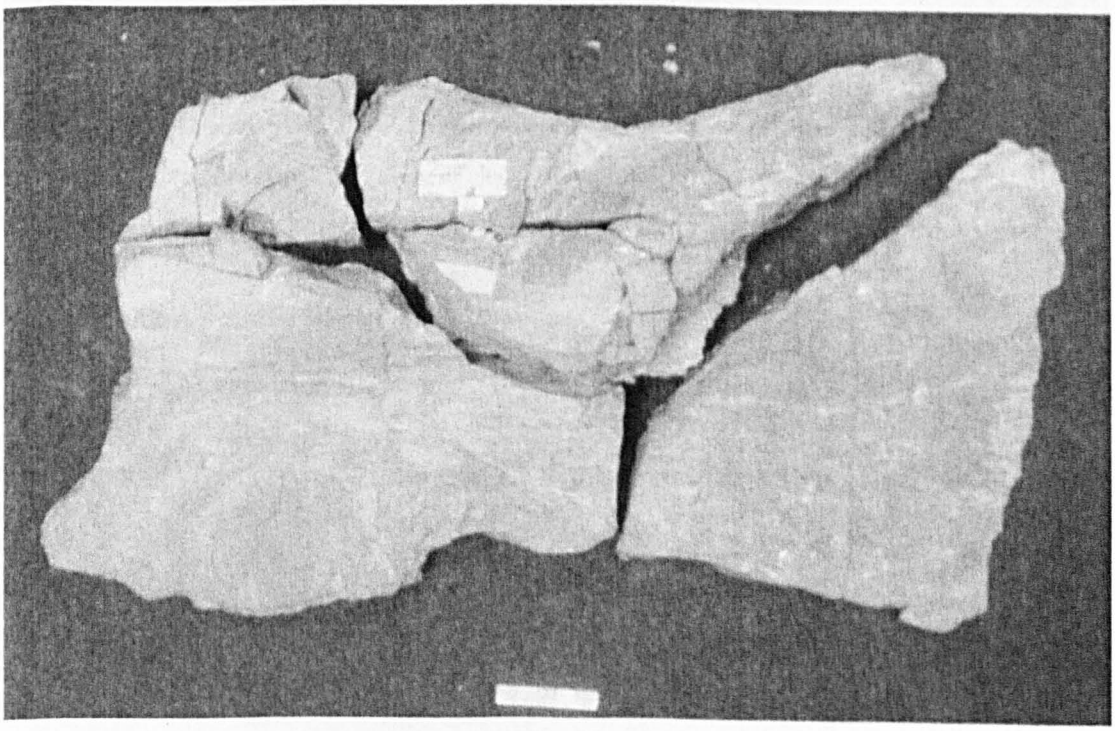


Figure 8.49. Partial heavily pyritised right hyomandibula (505mm x 260mm) from CAMSM J.46873a. Scale bar = 50mm.

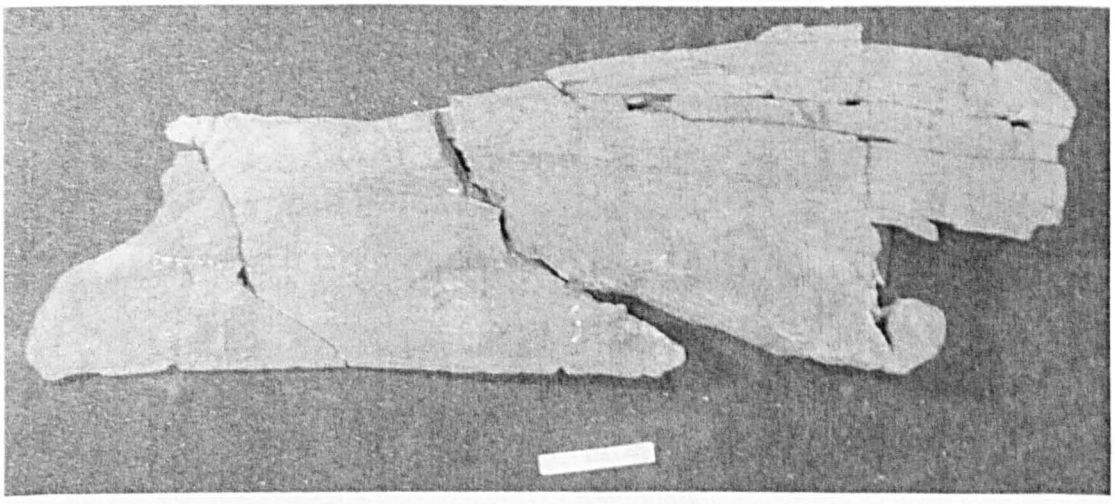


Figure 8.50. Pyritised right ceratohyal from BMNH P.10000. Scale bar = 50mm.

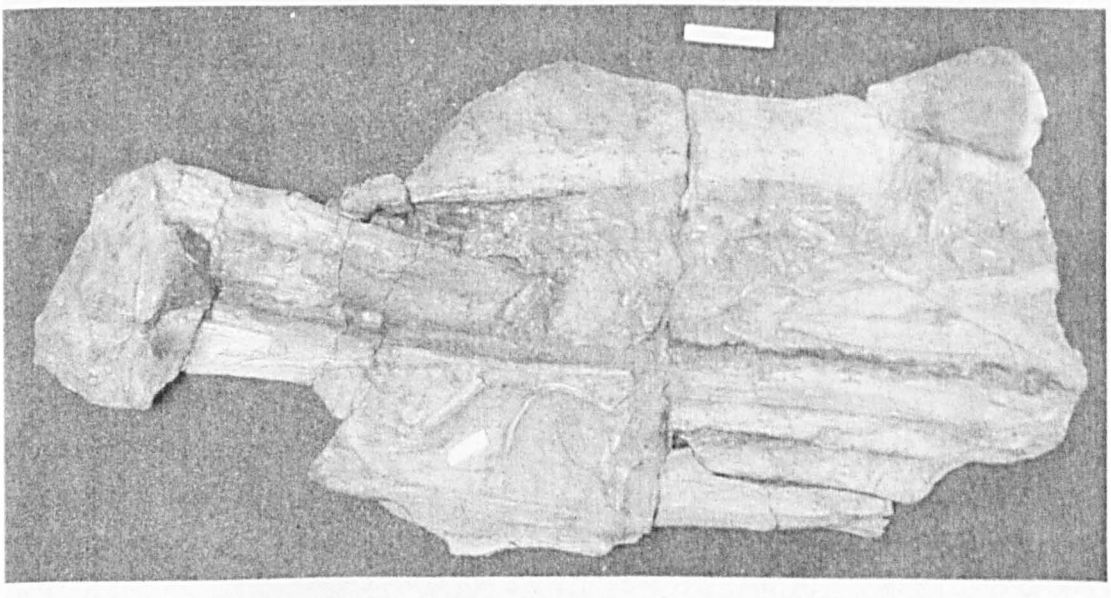


Figure 8.51a. Possible symplectic (at top of block) from LEICT G128.1900. Scale bar = 50mm.

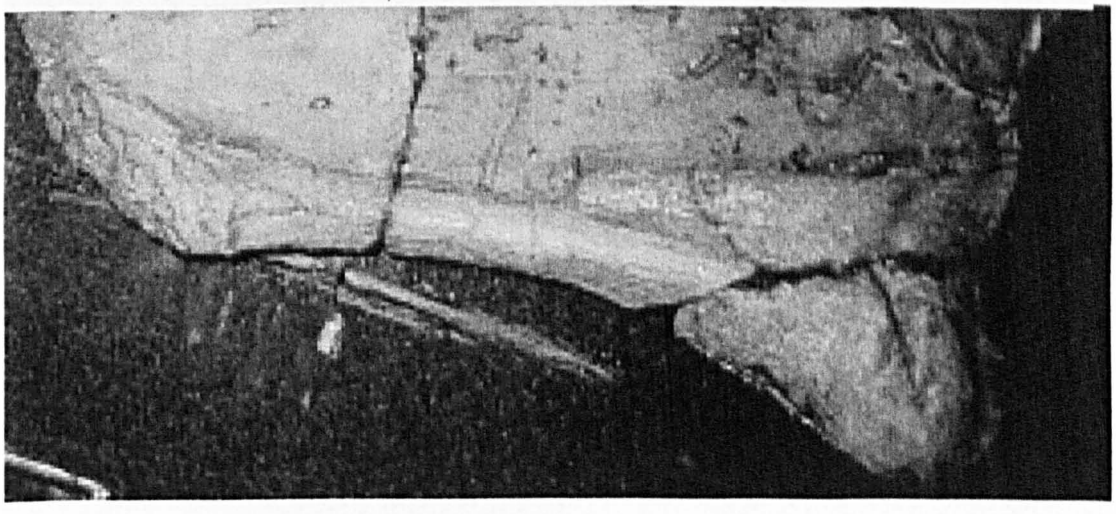


Figure 8.51b. Reverse side of possible symplectic from LEICT G128.1900.
Scale bar = 50mm.

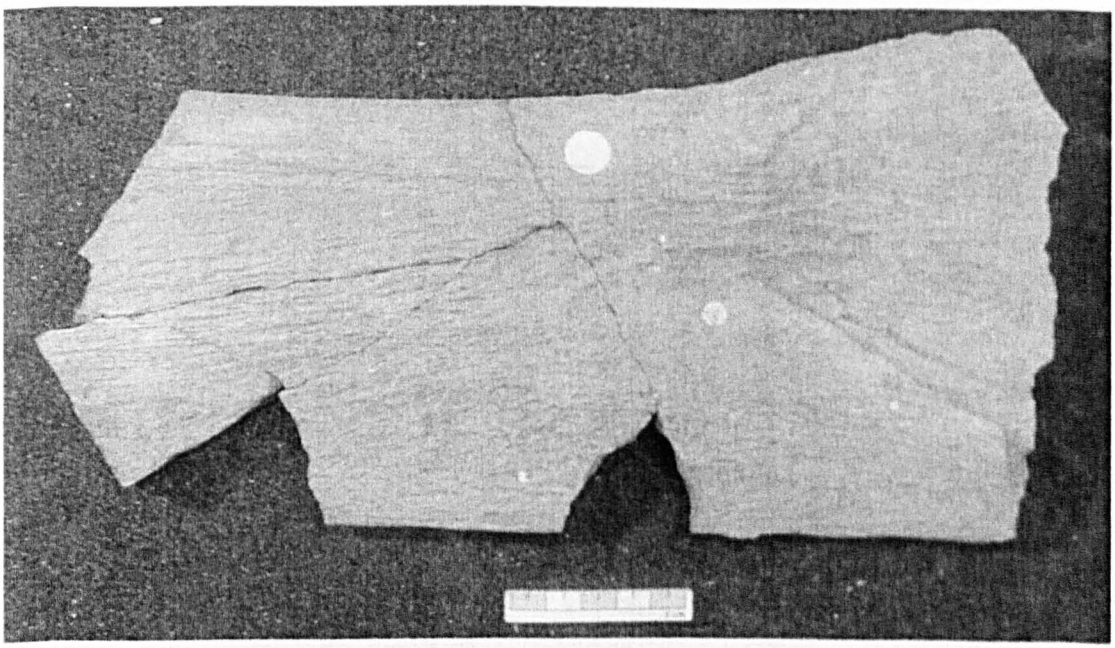


Figure 8.52. Left ceratohyal from BMNH P.6921, 290mm depth, lateral view.
Scale bar = 50mm.

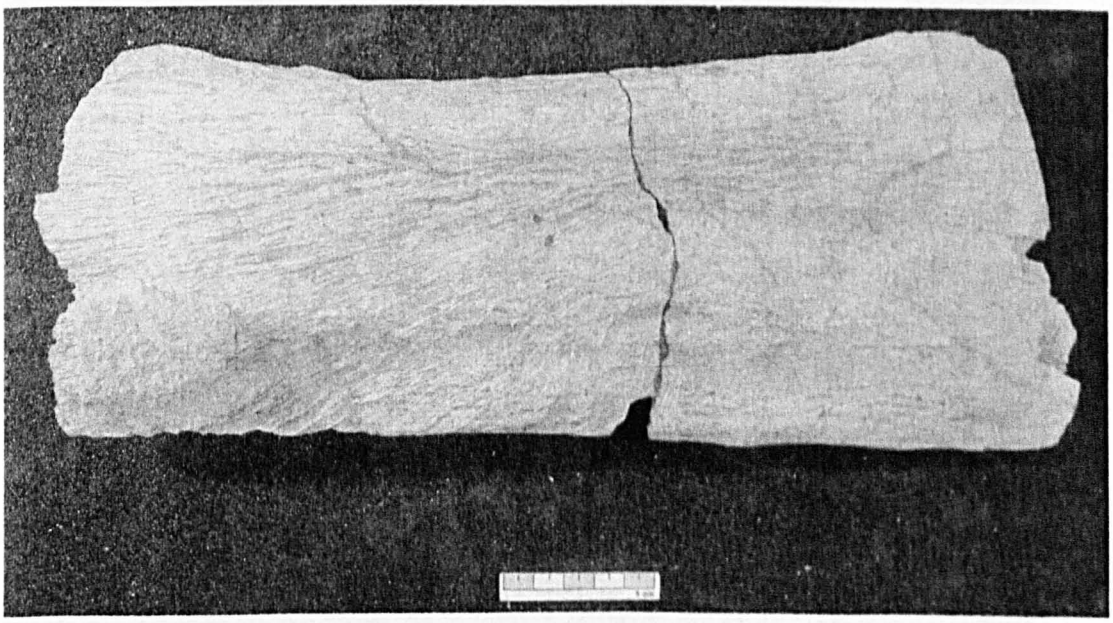


Figure 8.53. Left ceratohyal from GLAHM V3363, 141mm depth, lateral view.
Scale bar = 50mm.

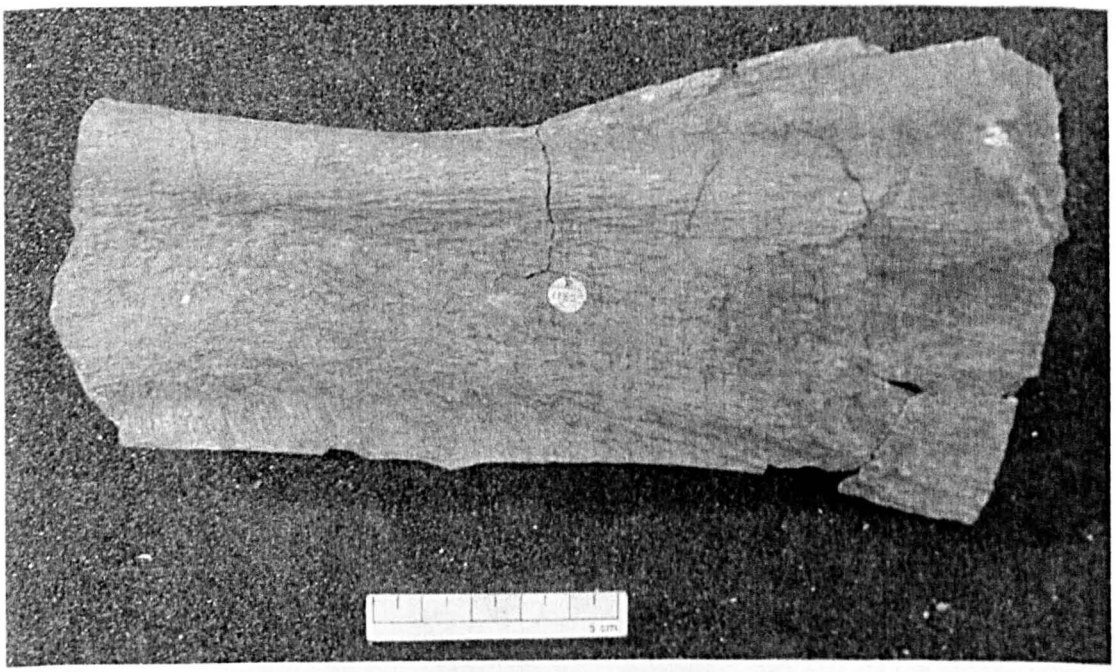


Figure 8.54. Right ceratohyal from BMNH P.11823, 66mm depth, lateral view. Scale bar = 50mm.

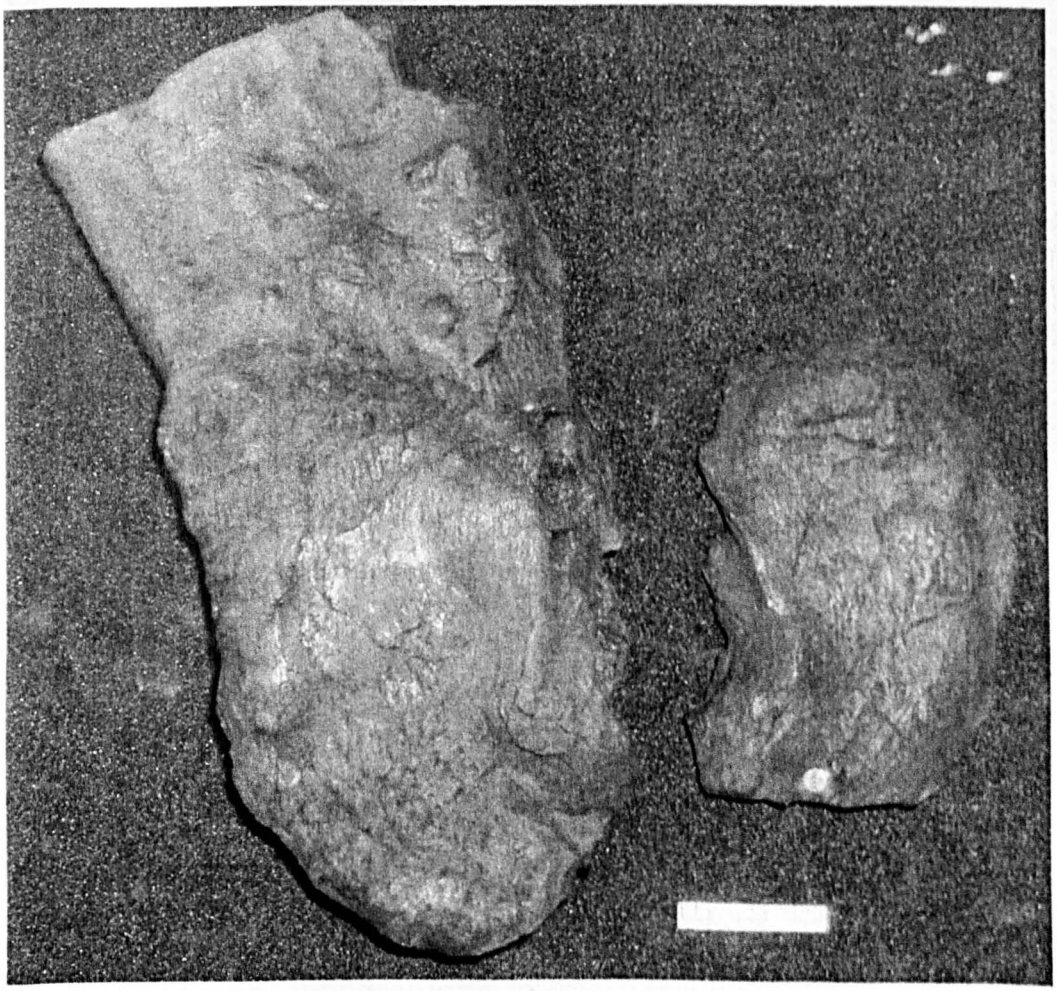


Figure 8.55a. Both hypohyals from BMNH P.10156, ventral view. Scale bar = 50mm.

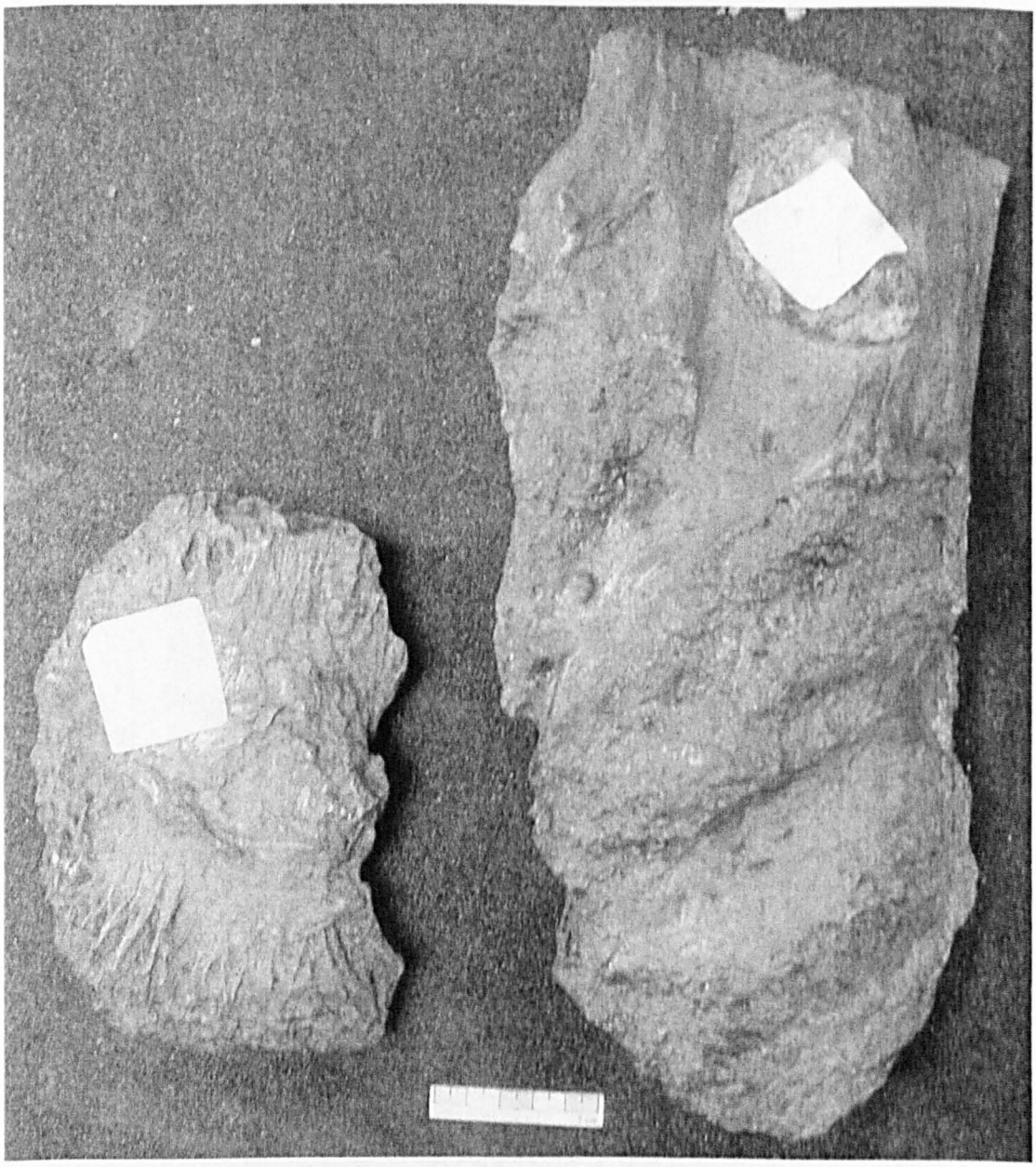


Figure 8.55b. Both hypohyals from BMNH P.10156, dorsal view. The left hypohyal (on the right) is almost entirely obscured by the bases of the first three hypobranchials. Scale bar = 50mm.

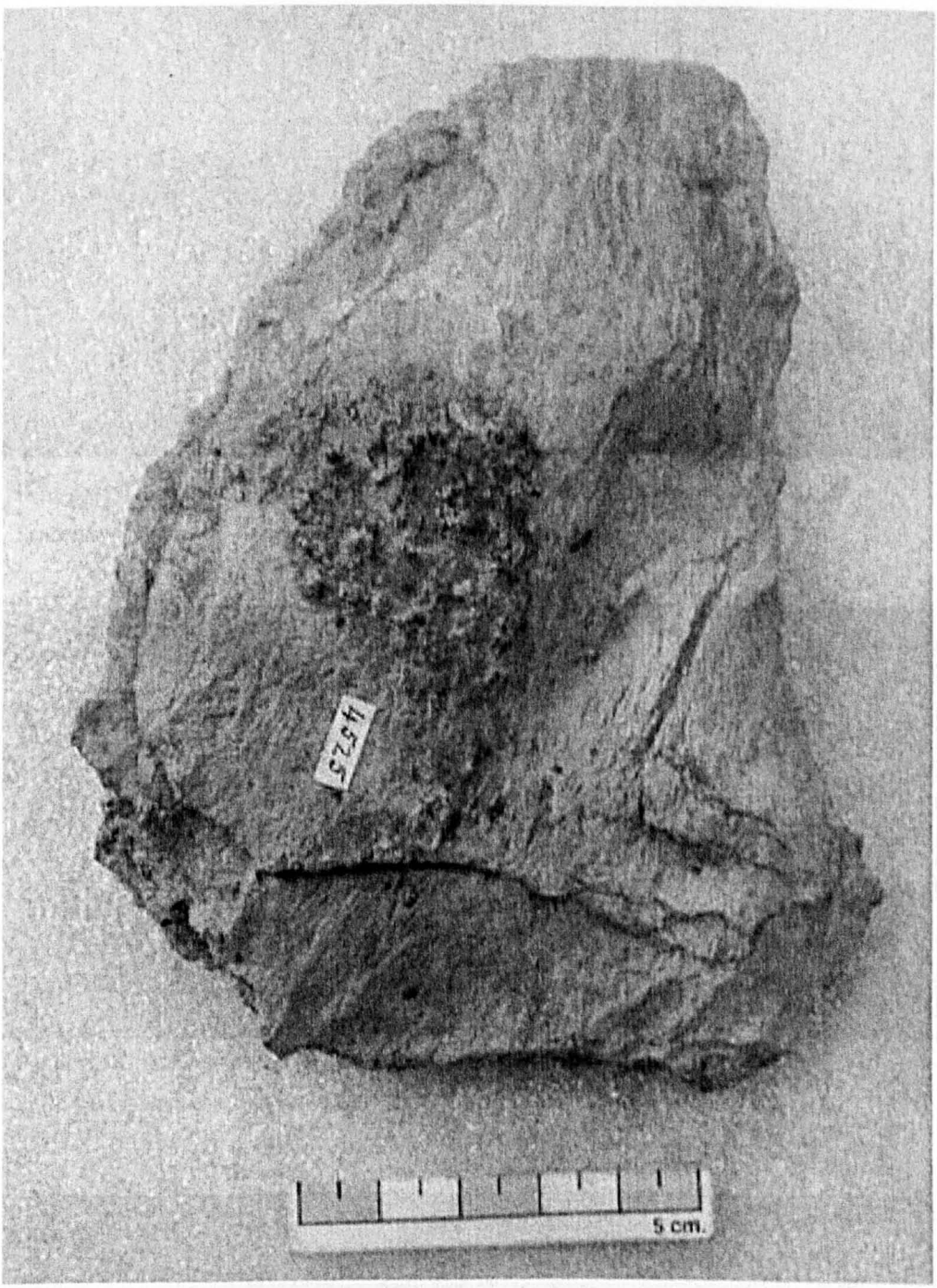


Figure 8.56. Left hypohyal (132mm long) from BMNH P.66340, ventral view.
Scale bar = 50mm.

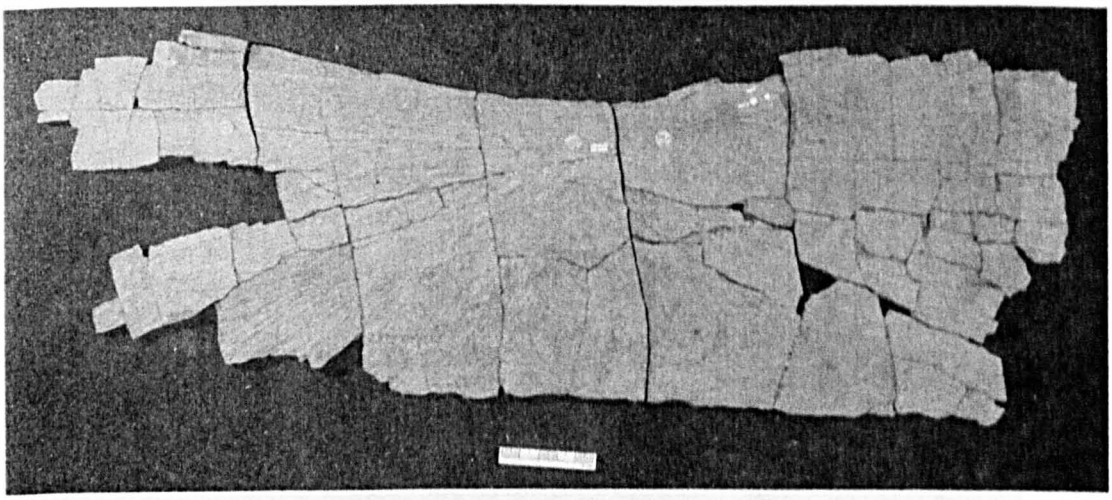


Figure 8.57. Left ceratohyal (591mm long) from BMNH P.47412, lateral view. Scale bar = 50mm.

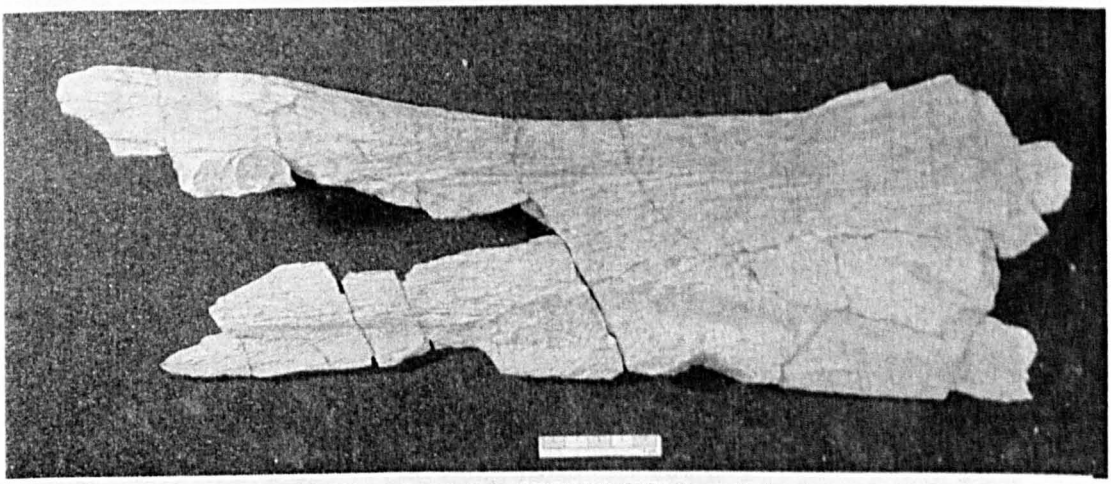


Figure 8.58. Left ceratohyal (439mm long) from BMNH P.6928, lateral view. Scale bar = 50mm.

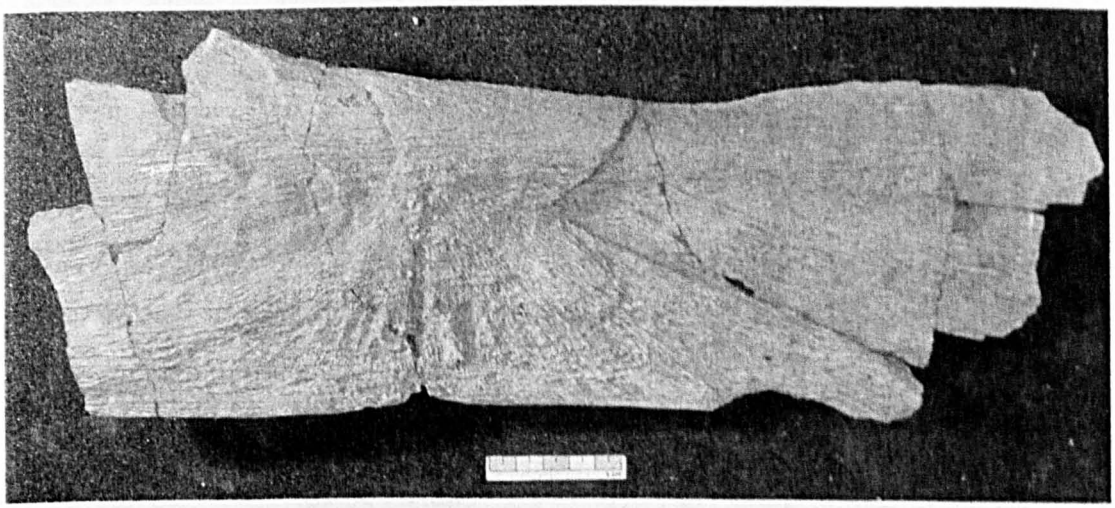


Figure 8.59. Right ceratohyal (402mm long) from CAMSM X.50114, lateral view. Scale bar = 50mm.

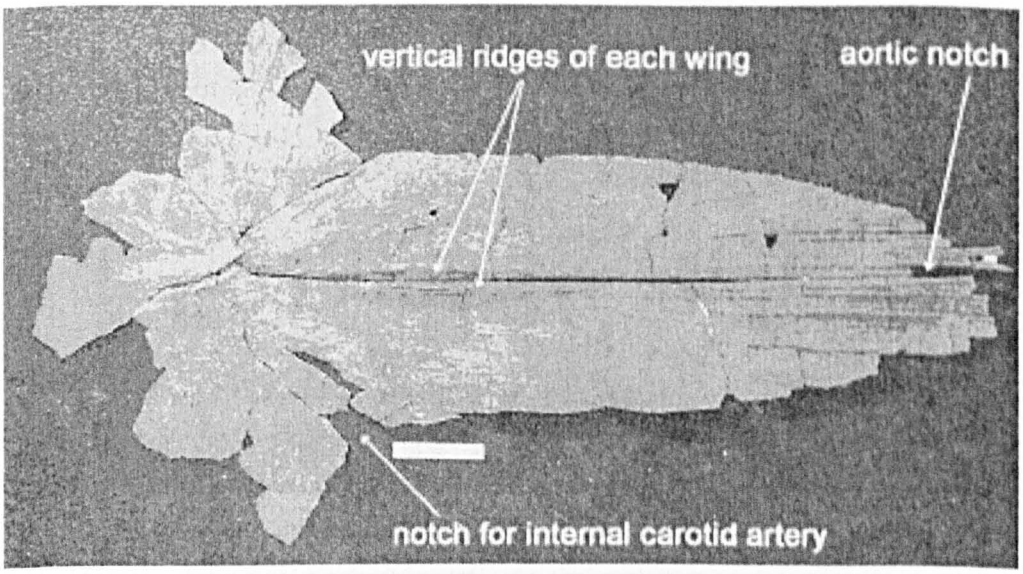


Figure 8.60. Parasphenoid (598mm long) from BMNH P.10000, dorsal view.
Scale bar = 50mm.

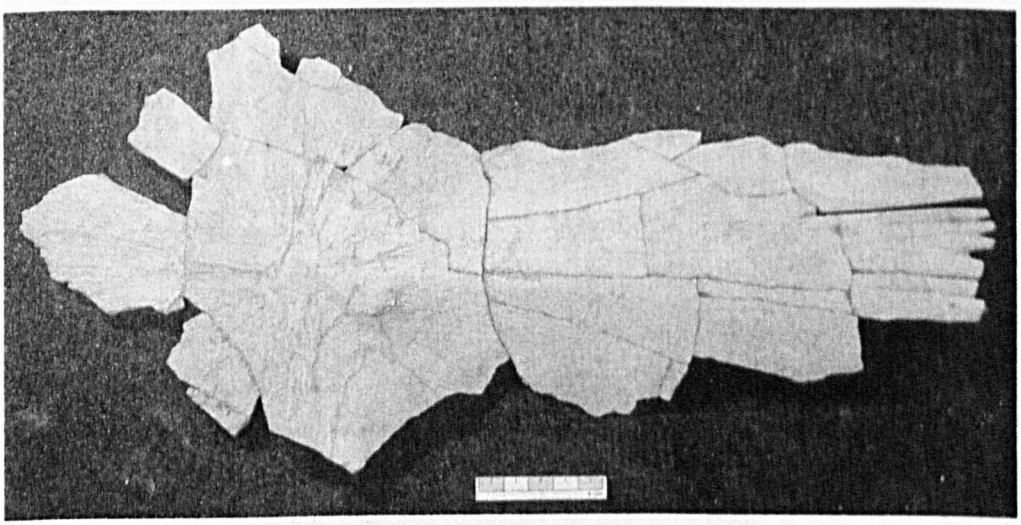


Figure 8.61a. Parasphenoid (404mm long) from LEICT G1.2005, ventral view.
Scale bar = 50mm.

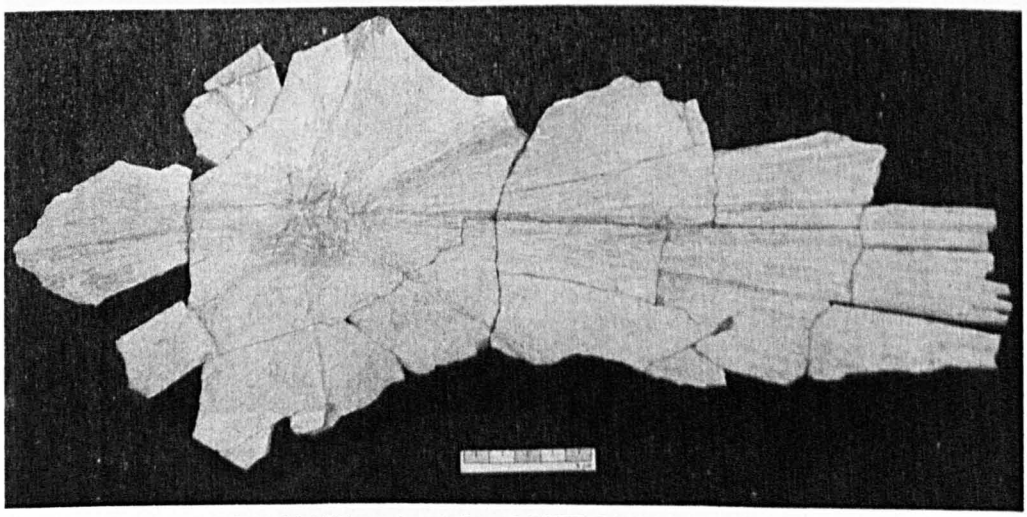


Figure 8.61b. Parasphenoid (404mm long) from LEICT G1.2005, dorsal view.
Scale bar = 50mm.

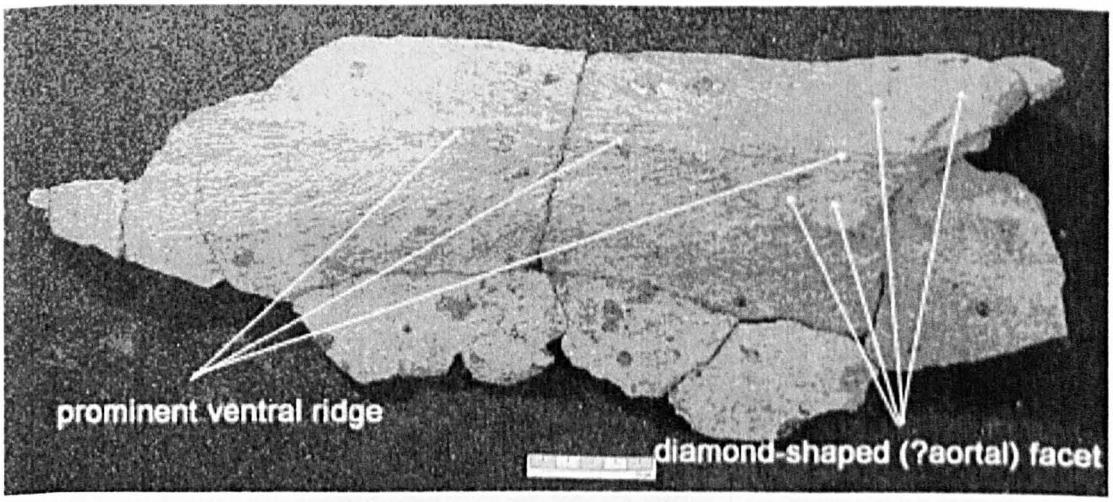


Figure 8.62a. Basiocciput from GLAHM V3363, ventrolateral view. Scale bar = 50mm.

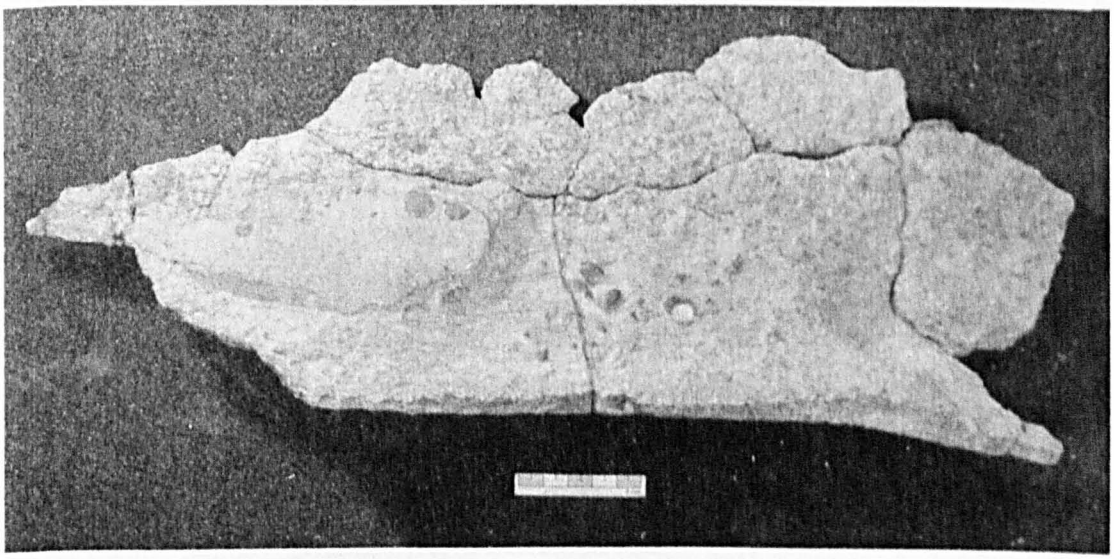


Figure 8.62b. Basiocciput from GLAHM V3363, dorsolateral view. Scale bar = 50mm.

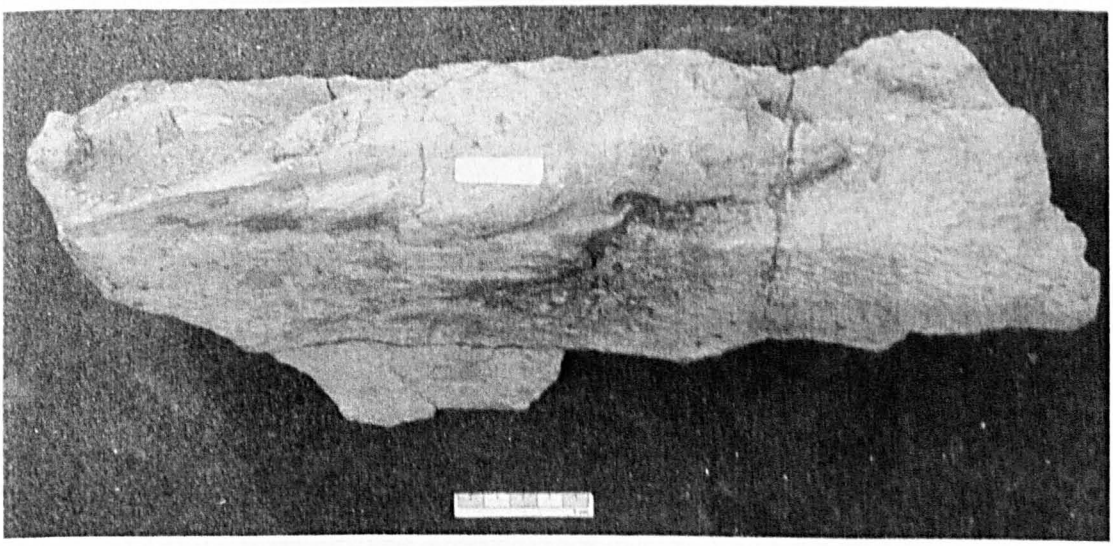


Figure 8.62c. Basiocciput from LEICT G128.1900, ventrolateral view. Note possible prootic prong overlying surface of bone. Scale bar = 50mm.

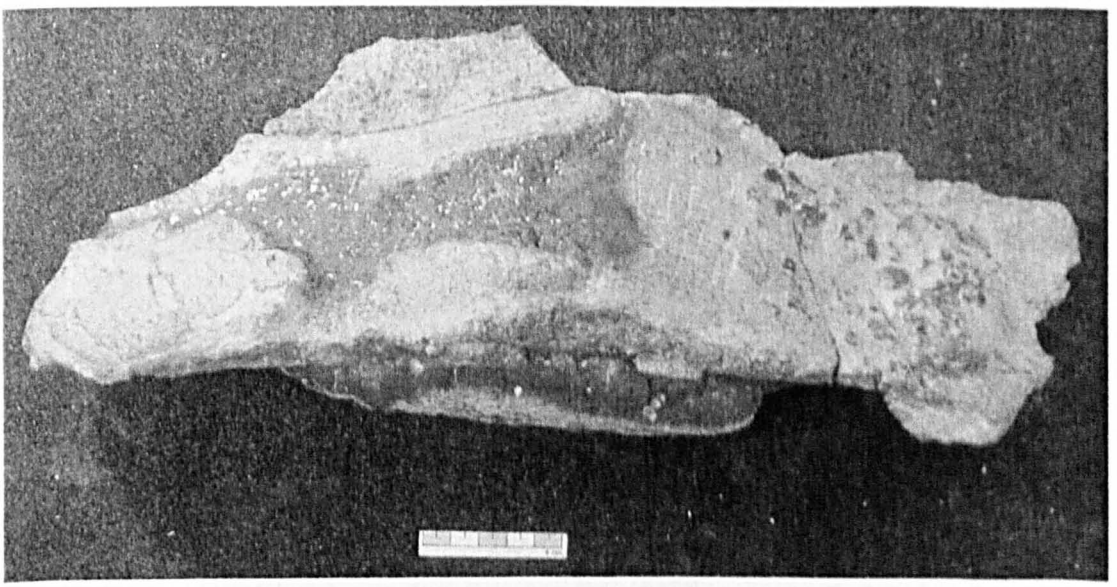


Figure 8.62d. Basioccipiut from LEICT G128.1900, dorsolateral view.
Scale bar = 50mm.

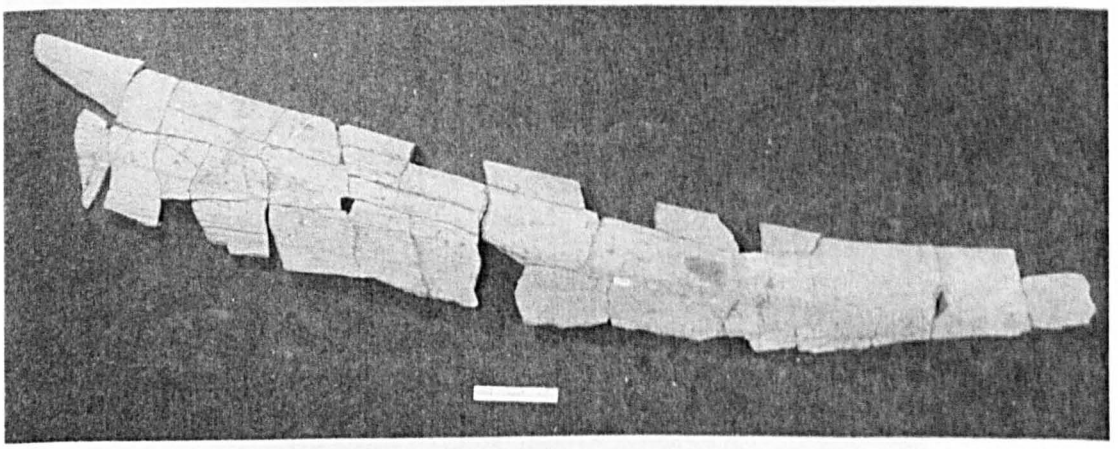


Figure 8.63a. Right dentary, 737mm long, from BMNH P.66340, external view.
Scale bar = 50mm.

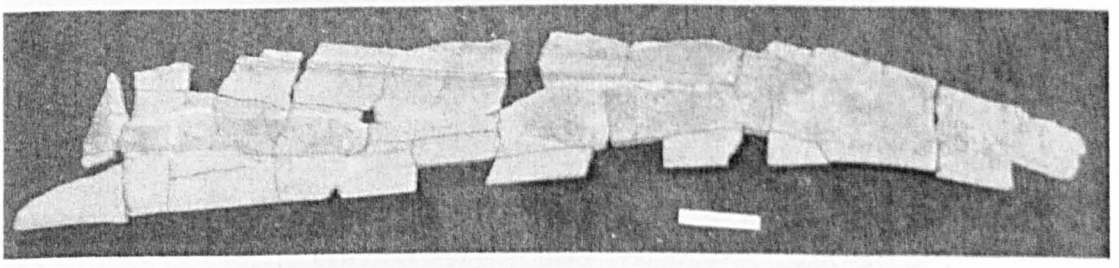


Figure 8.63b. Right dentary, 737mm long, from BMNH P.66340, internal view.
Scale bar = 50mm.

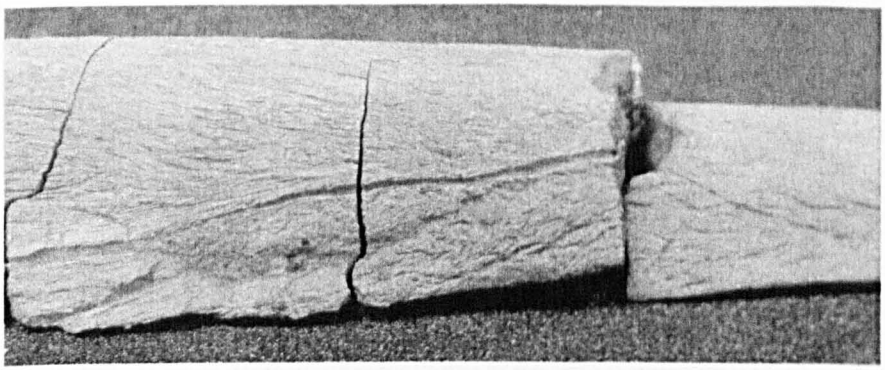


Figure 8.63c. Right dentary, detail, showing mandibular sensory canal, external view. Scale bar = 50mm.

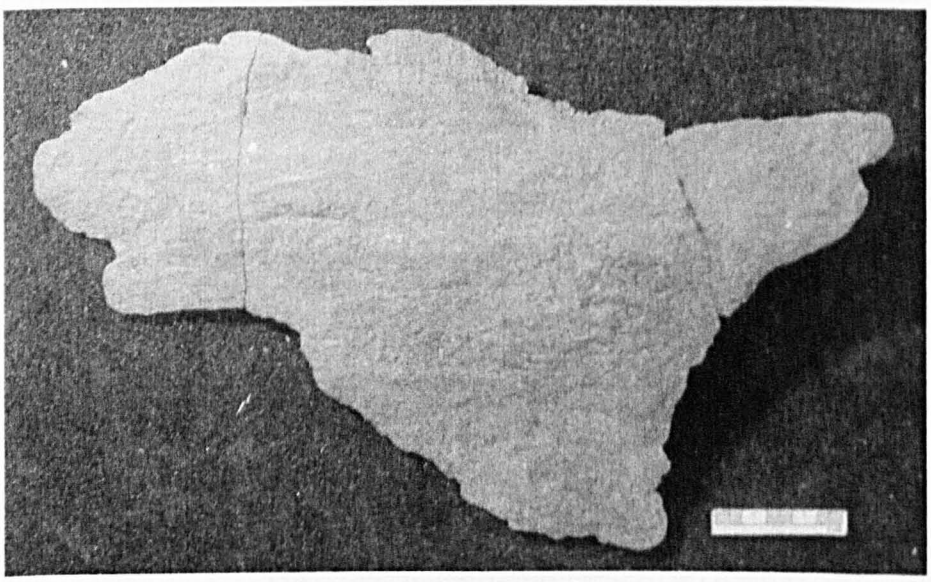


Figure 8.64a. Left dermosphenotic, from BMNH P.12534, external view.
Scale bar = 50mm.

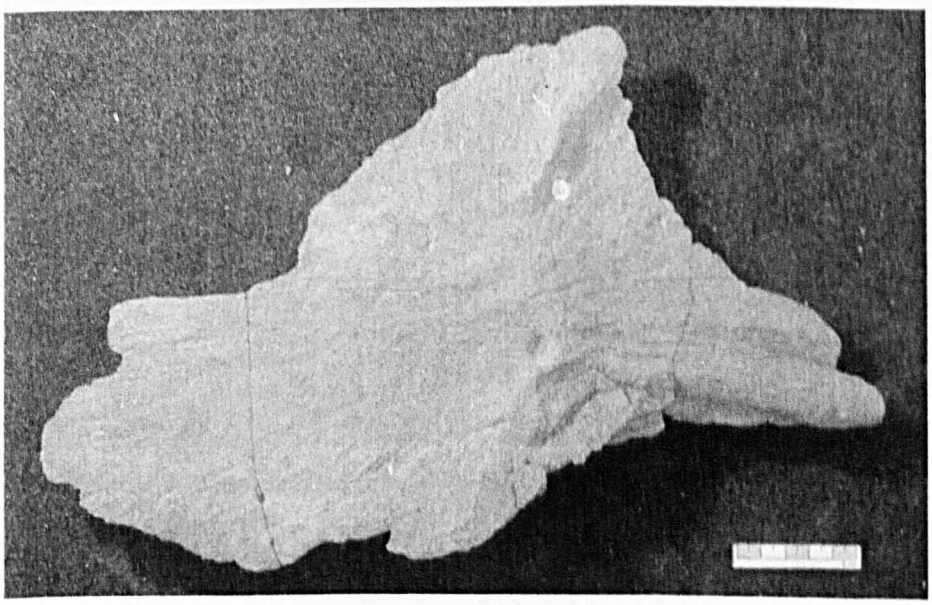


Figure 8.64b. Left dermosphenotic, from BMNH P.12534, internal view.
Scale bar = 50mm.

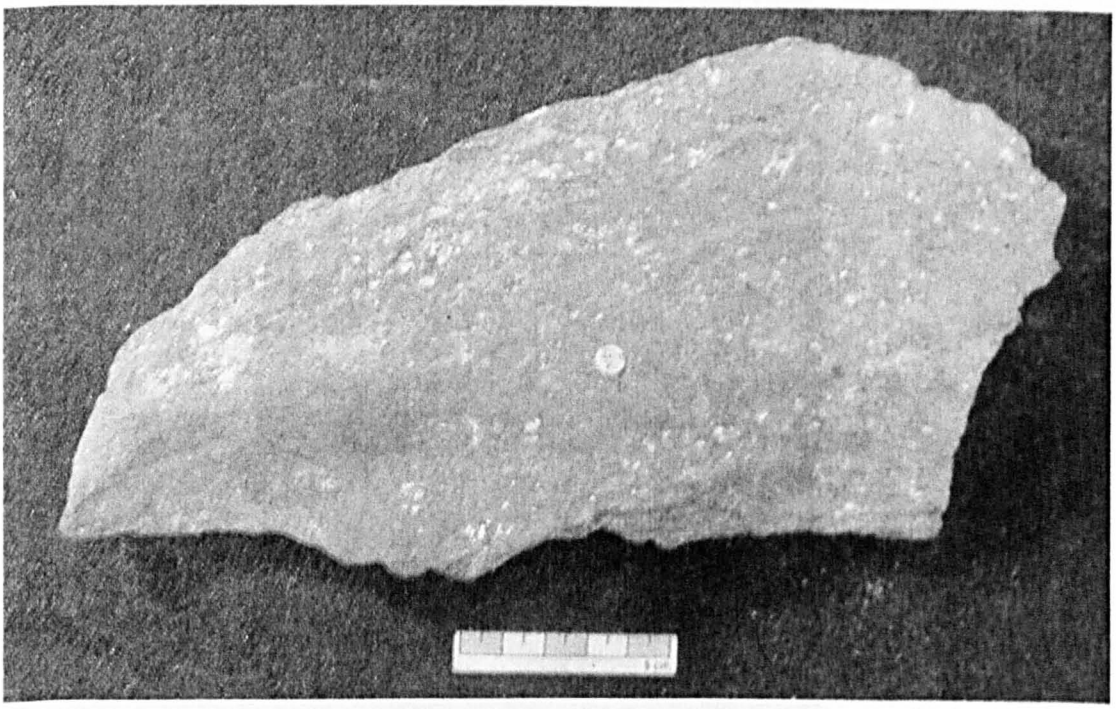


Figure 8.65a. Left supramaxilla, from BMNH P. 6930, external view.
Scale bar = 50mm.

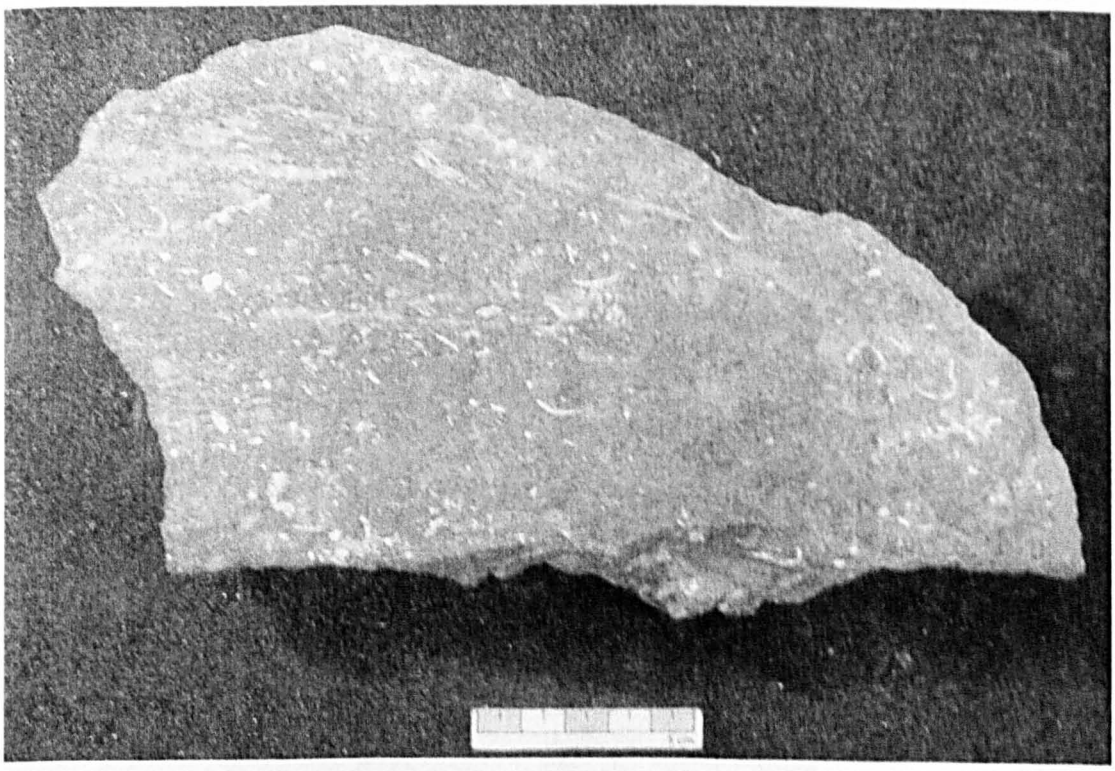


Figure 8.65b. Left supramaxilla, from BMNH P. 6930, internal view.
Scale bar = 50mm.

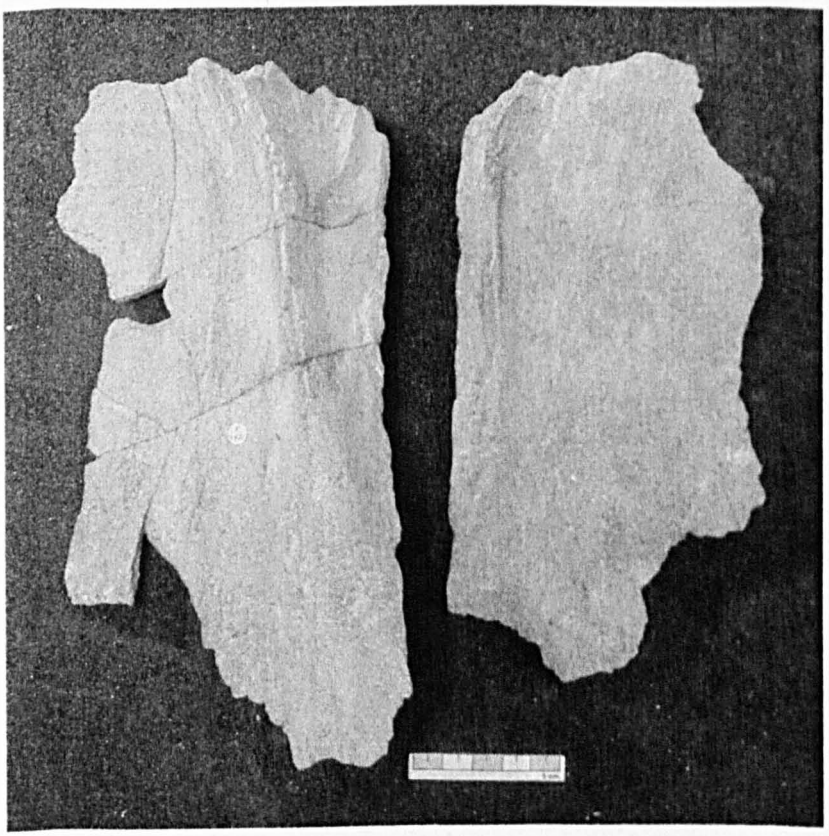


Figure 8.66a. Paired nasals, from BMNH P.6930, dorsal view. Scale bar = 50mm.

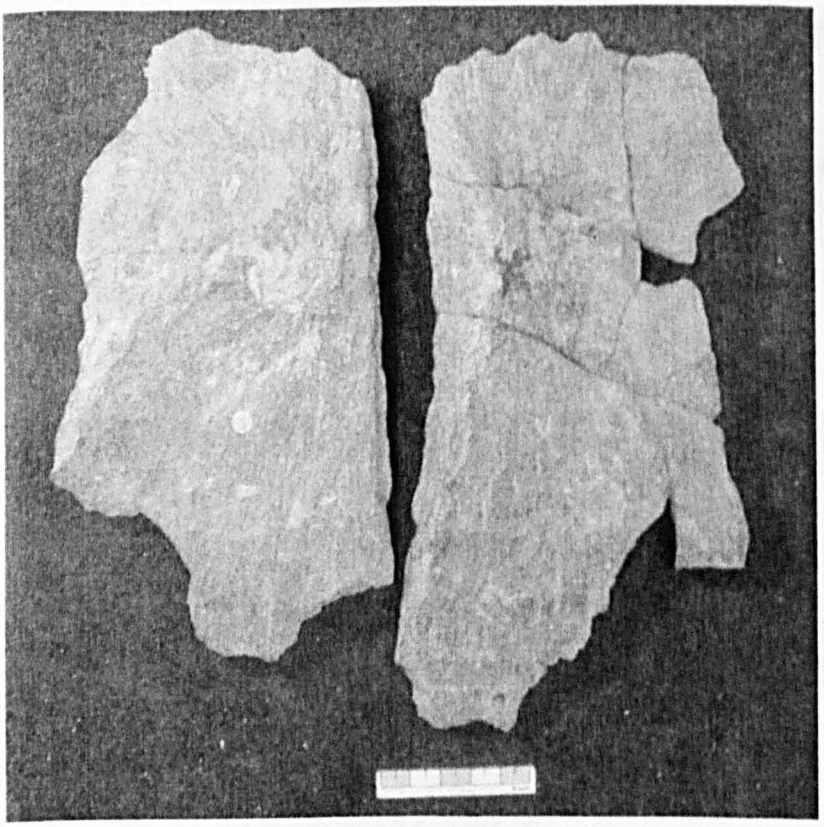


Figure 8.66b. Paired nasals, from BMNH P.6930, ventral view. Scale bar = 50mm.

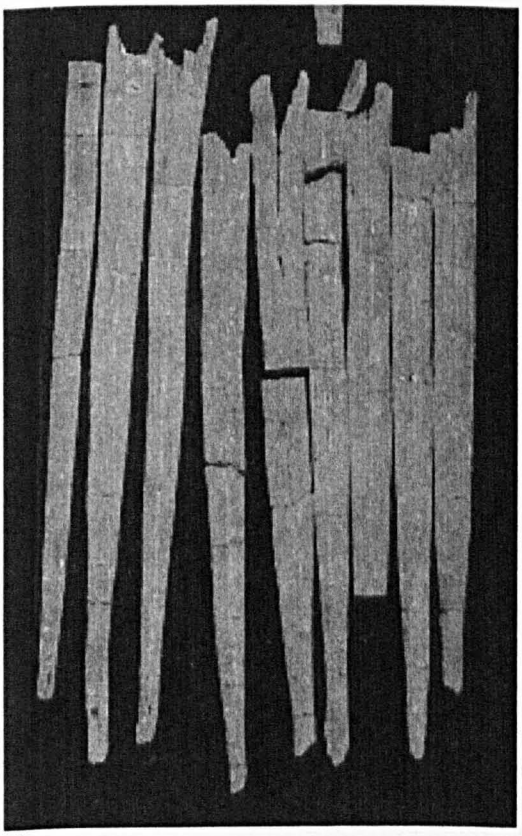


Figure 8.67a. Series of proximal radials for the dorsal fin, from GLAHM V3363. Longest measures 703mm.

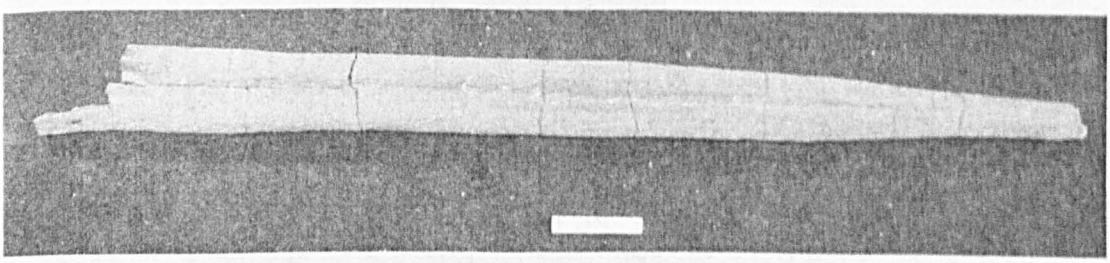


Figure 8.67b. Proximal radial for the dorsal fin, 703mm long, from GLAHM V3363. Scale bar = 50mm.

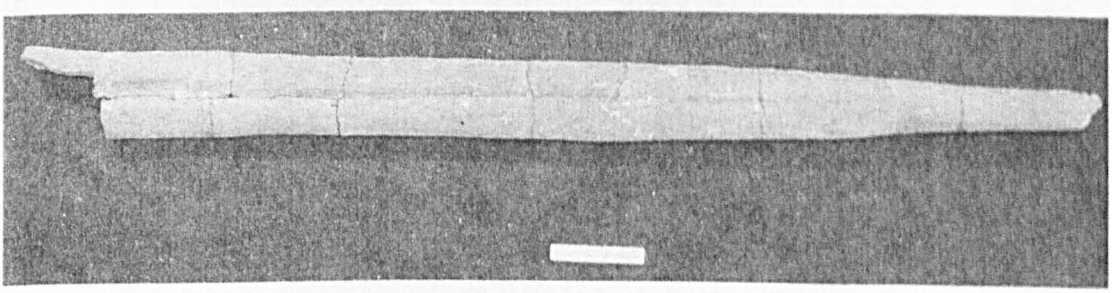


Figure 8.67c. Proximal radial for the dorsal fin, 703mm long, from GLAHM V3363, reverse view. Scale bar = 50mm.

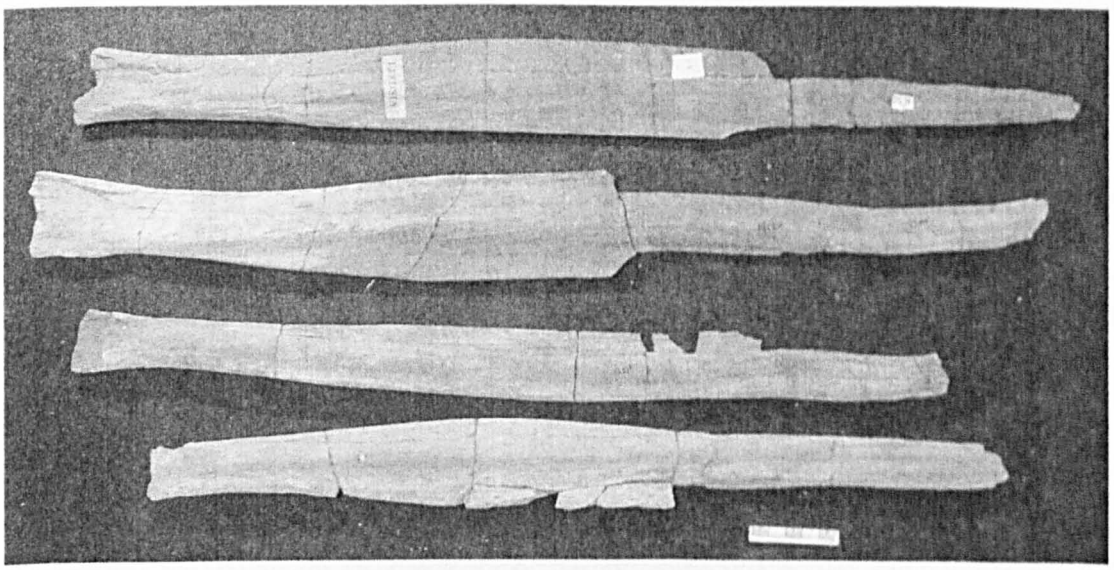


Figure 8.68a. Series of four anal fin supports, from GLAHM V3363. Scale bar = 50mm.

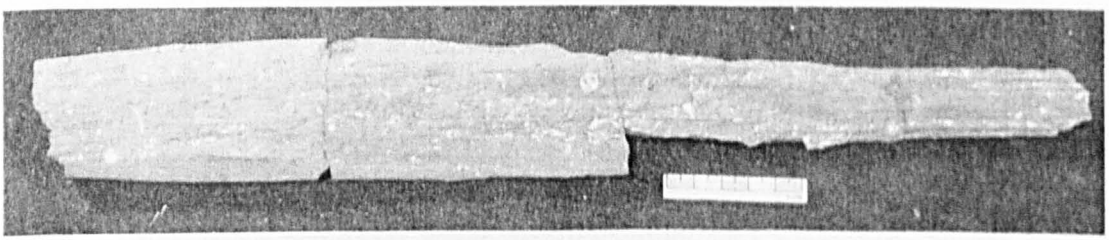


Figure 8.68b. Partial right anal fin support fragment, from BMNH P.6928. Scale bar = 50mm.

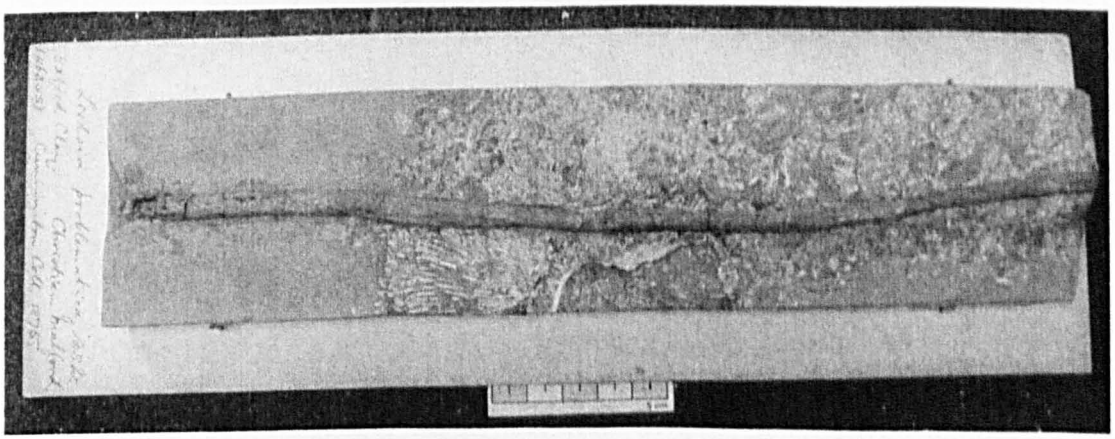


Figure 8.69. Isolated fin-ray fragment from Christian Malford, Wiltshire, BMNH 46355. Scale bar = 50mm.

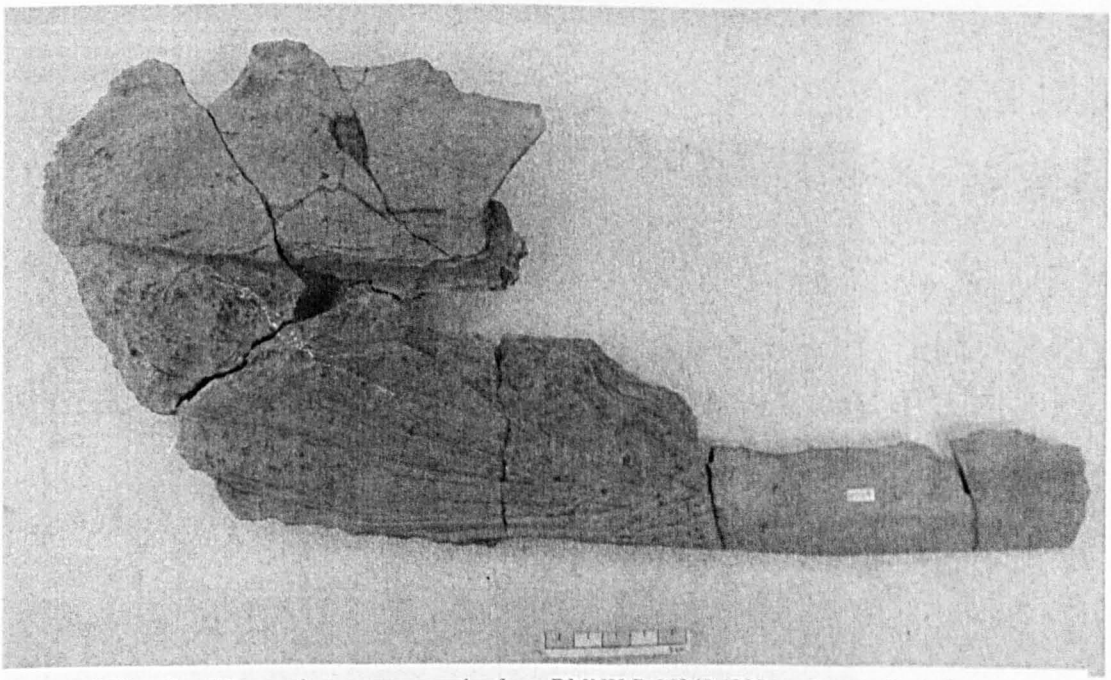


Figure 8.70a. Possible angular or supraangular from BMNH P.66340 (330mm long). Scale bar = 50mm.

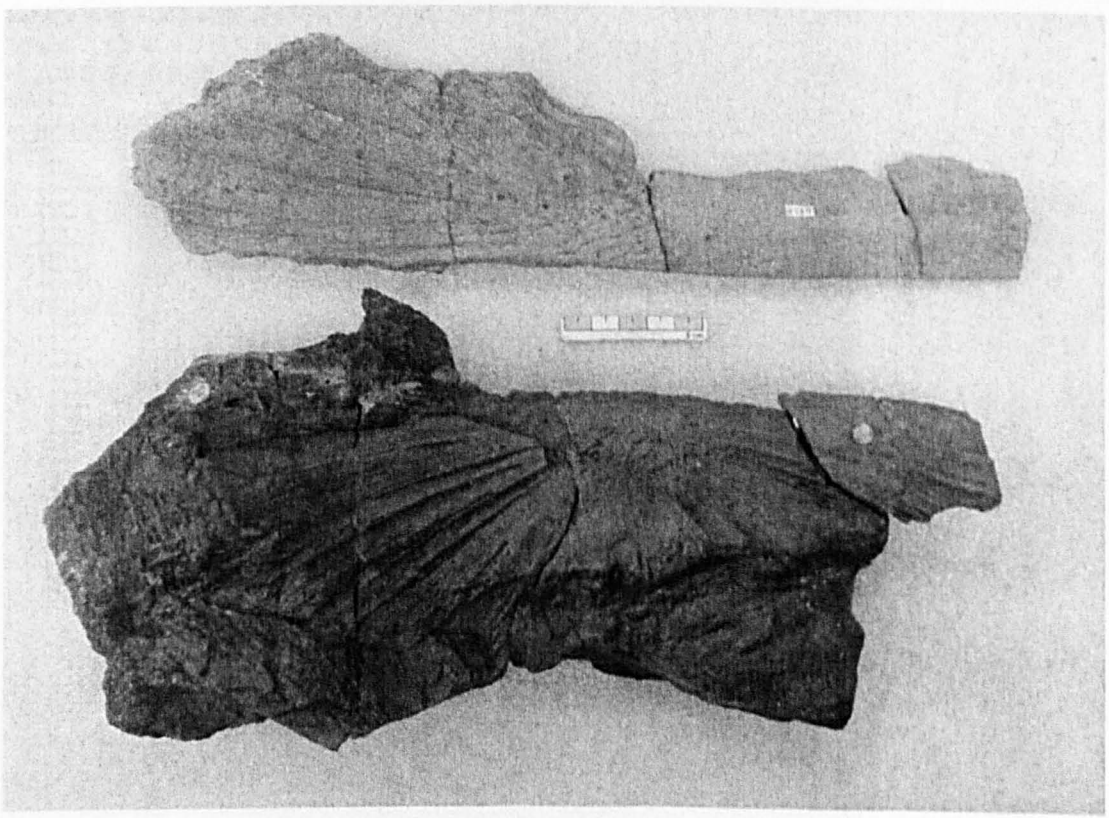


Figure 8.70b. Possible angular or supraangular from BMNH P.66340 compared to same element in BMNH P.10156/3 (328mm long). Scale bar = 50mm.

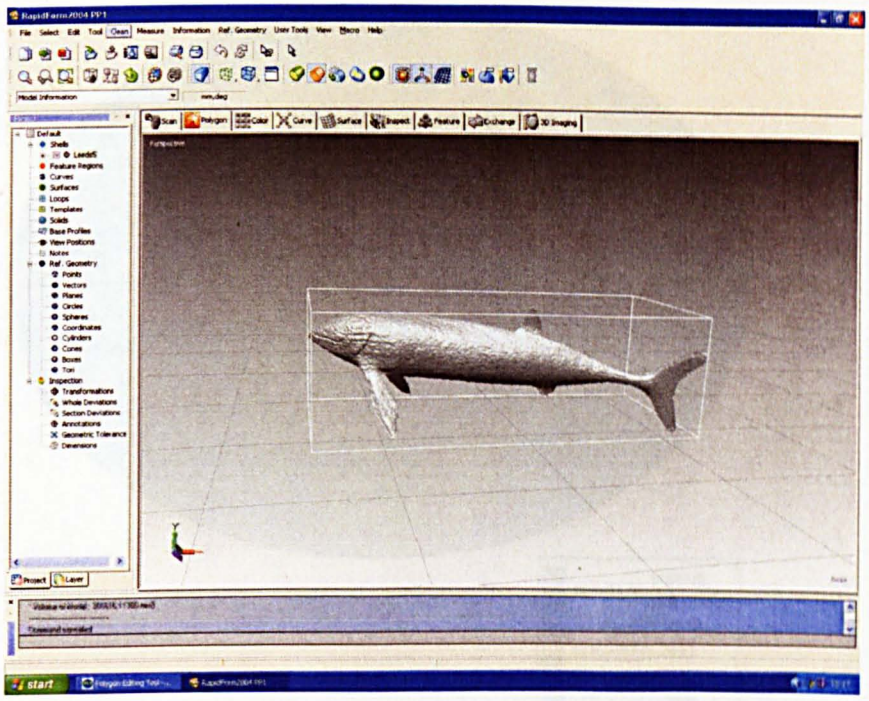


Figure 9.1a. Reconstruction of *Leedsichthys* by Bob Nicholls, scanned by RapidForm and analysed by MIMICS, lateral view. Image courtesy of Stig Walsh.

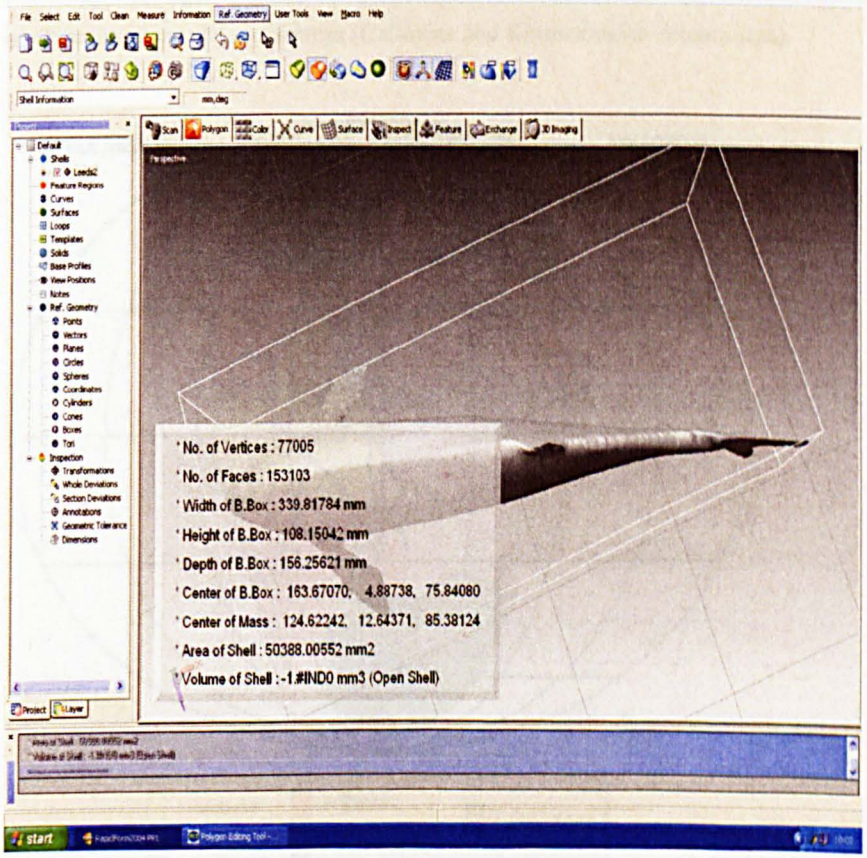


Figure 9.1b. Reconstruction of *Leedsichthys* by Bob Nicholls, scanned by RapidForm and analysed by MIMICS, plan view. Image courtesy of Stig Walsh.

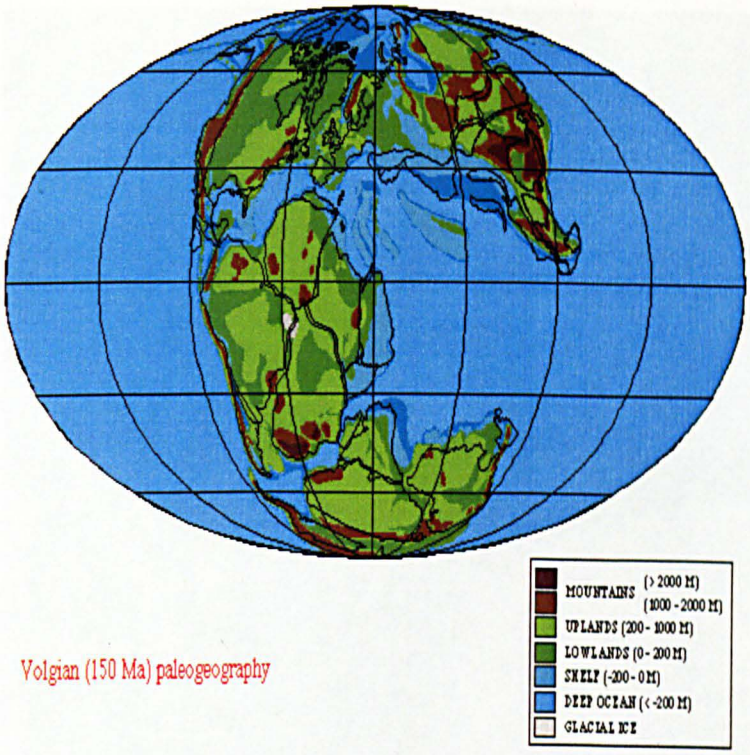


Figure 9.2a. Middle Jurassic palaeogeography (from Fig.10.8A of Rees *et al.* 2000), showing Tetho-Caribbean Seaway connecting southern province of *Leedsichthys* (Oxfordian occurrences) with the northern province of *Leedsichthys* (Callovian and Kimmeridgian occurrences).

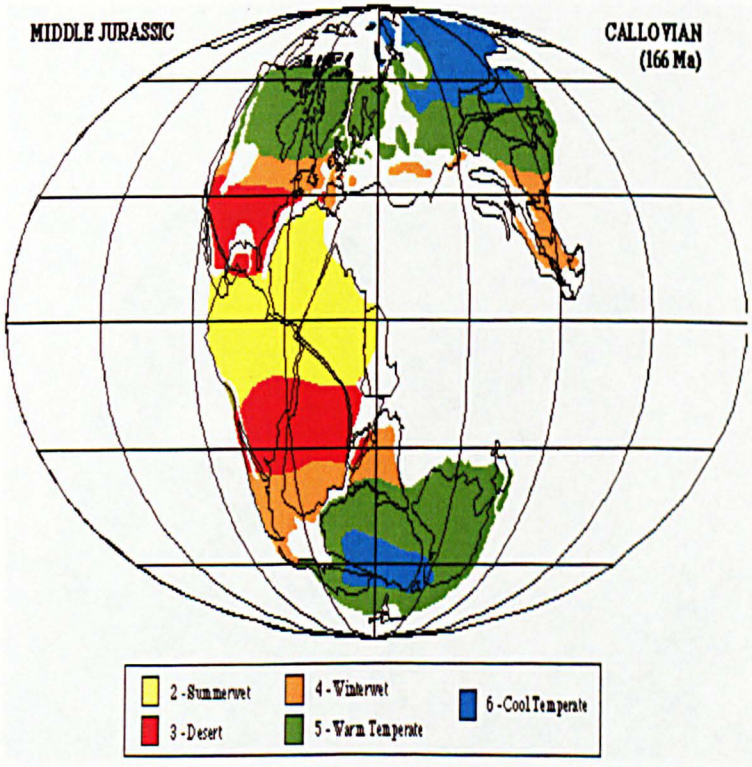


Figure 9.2b. Middle Jurassic terrestrial climate belts (from Fig.7B of Rees *et al.* 2000), showing possible influence of terrigenous influx in areas relating to *Leedsichthys* provinces.

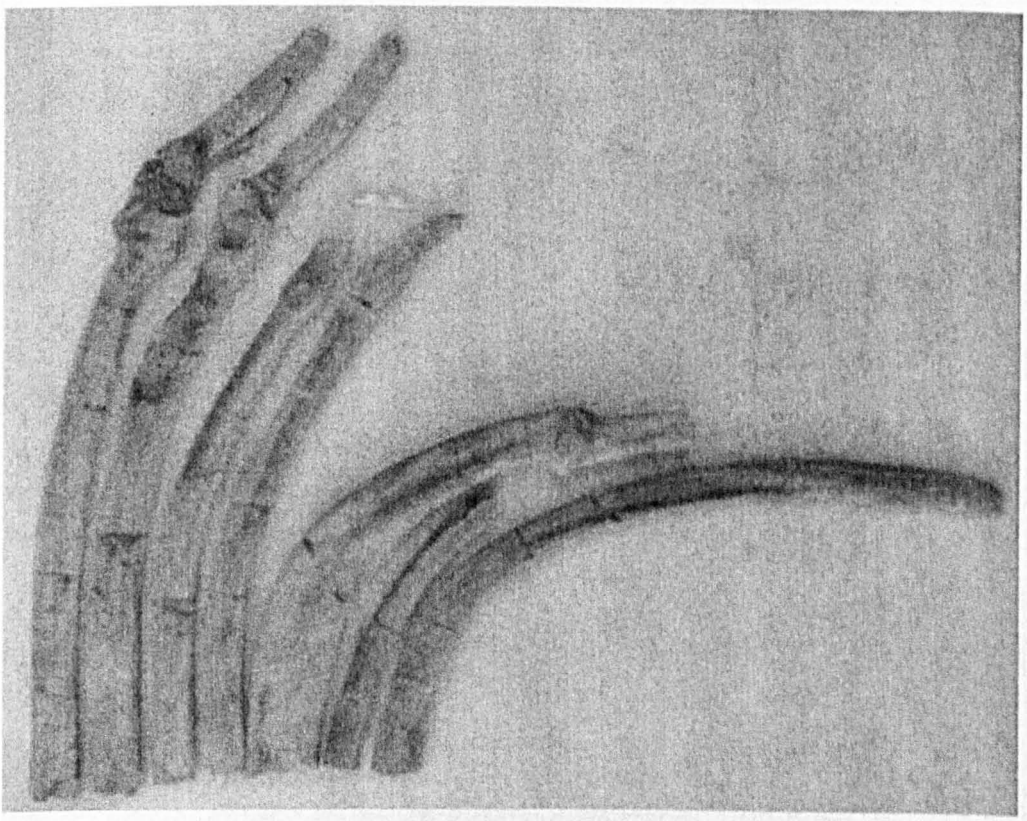


Figure 9.3a. BMNH P.6924, dorsal fin-rays, showing callus growth following apparent attack. Scale bar = 50mm.

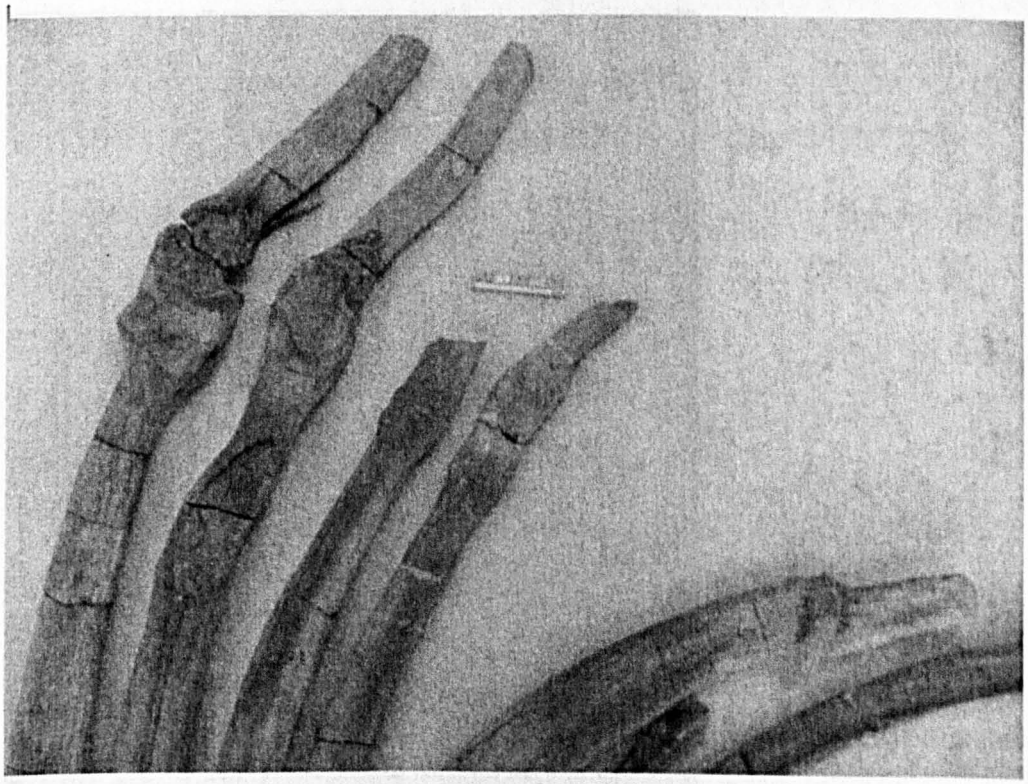


Figure 9.3b. BMNH P.6924, dorsal fin-rays, detail, with crush marks in the two fin-rays to the left of the image. Extreme left fin-ray shows signs of possible circular dent by a tooth crown, and a straight line of damage is traceable across the three following fin-rays. The fin-ray second from the left shows a second impression, possibly indicating the opposite side of the jaw inflicting the straight line of damage. Scale bar = 50mm.

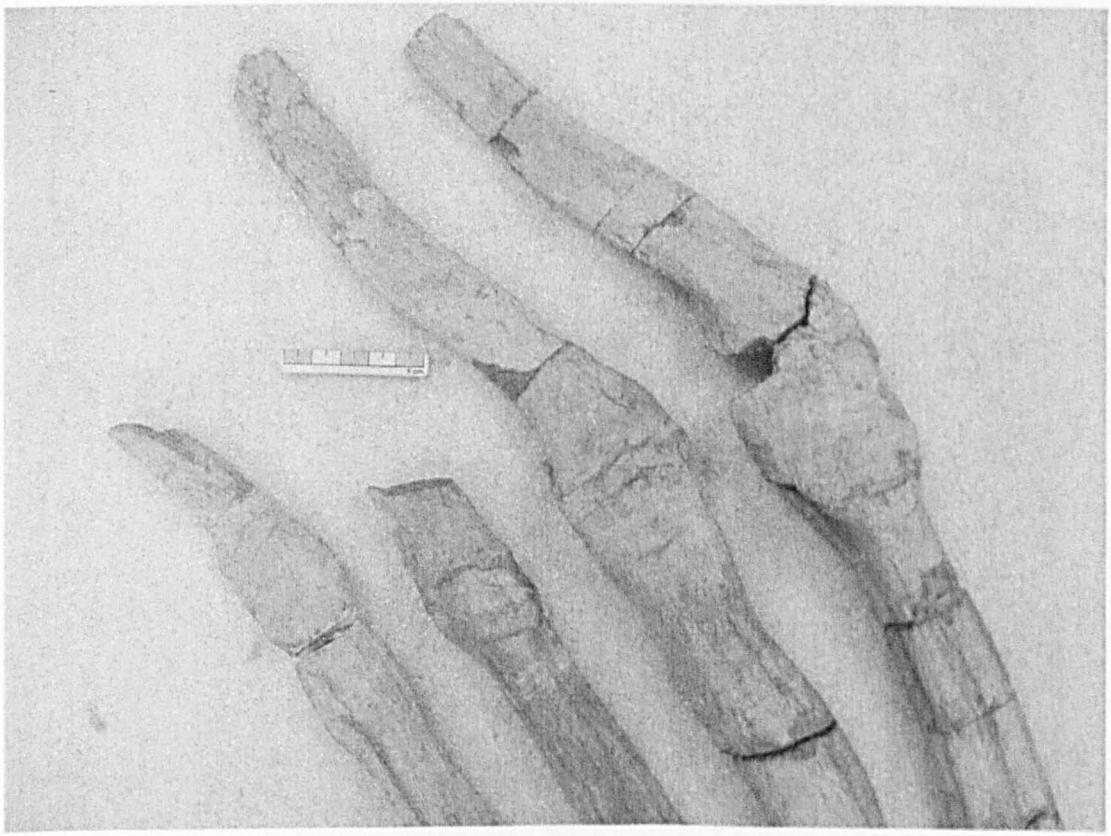


Figure 9.3c. BMNH P.6924, dorsal fin-rays, detail, reverse view, showing distortion of bone and callus growth. Scale bar = 50mm.

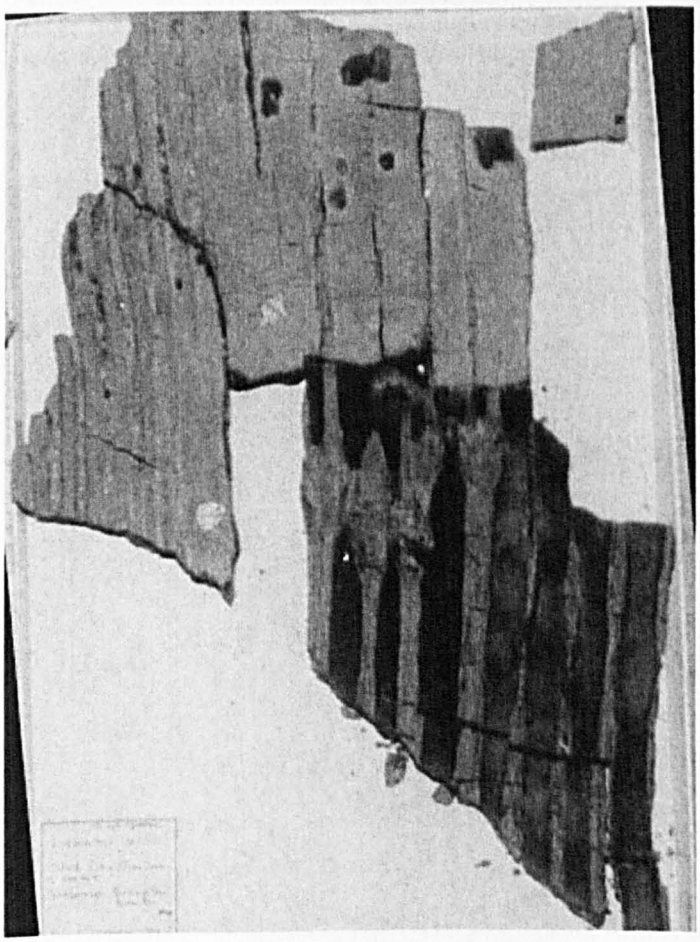


Figure 9.3d. BMNH P.62054, fin-rays. Note arc of callus growth and breaks in central four fin-rays. The connective tissue of the fin would have held the rays in position while bone growth repaired the damage. Specimen is 150mm across.

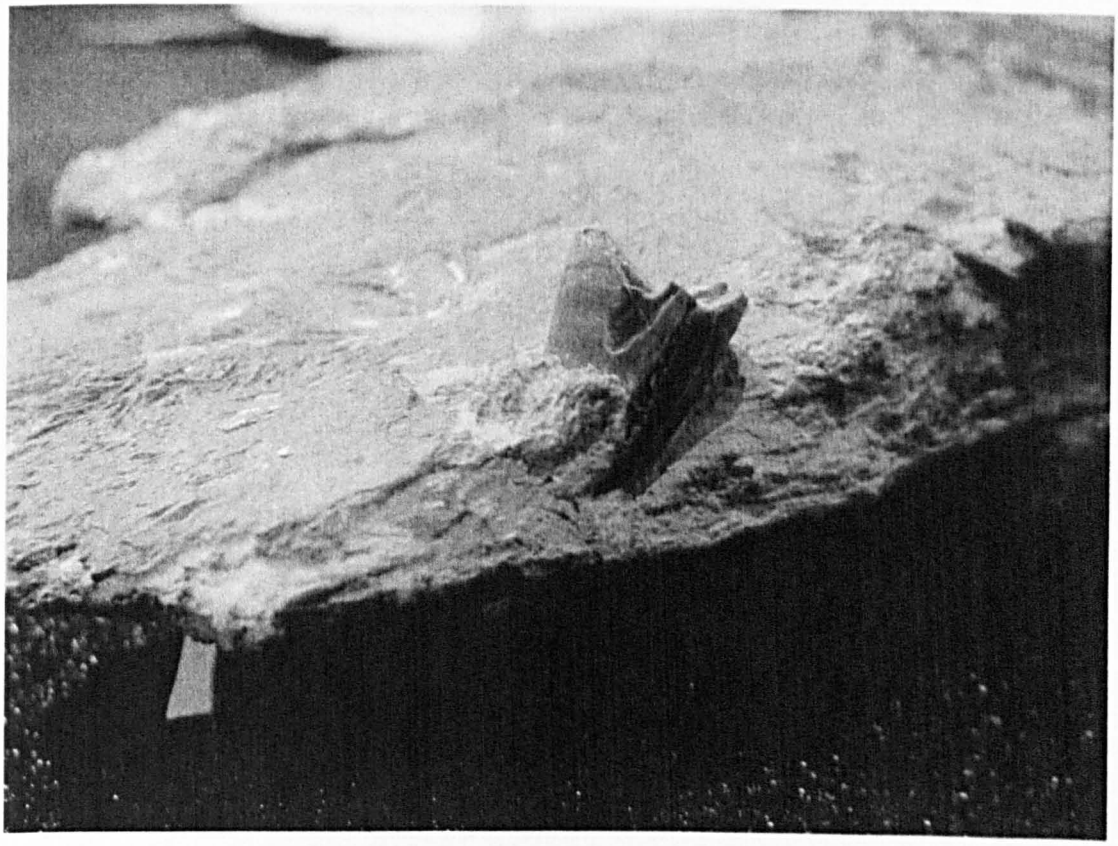


Figure 9.4. PETMG F1, portion of hyomandibula with crocodilian tooth imbedded in it, and clay infilling some of the surrounding area. Note that the only area of possible bone regrowth from this wound is (in image) on the near-side of the tooth, and this tissue is folds at the top, as though folded back. Bone growth would form a solid callus of cells for repair, rather than this folded layer which is more suggestive of bone deforming plastically from the tooth impact. Tooth is 43mm long.

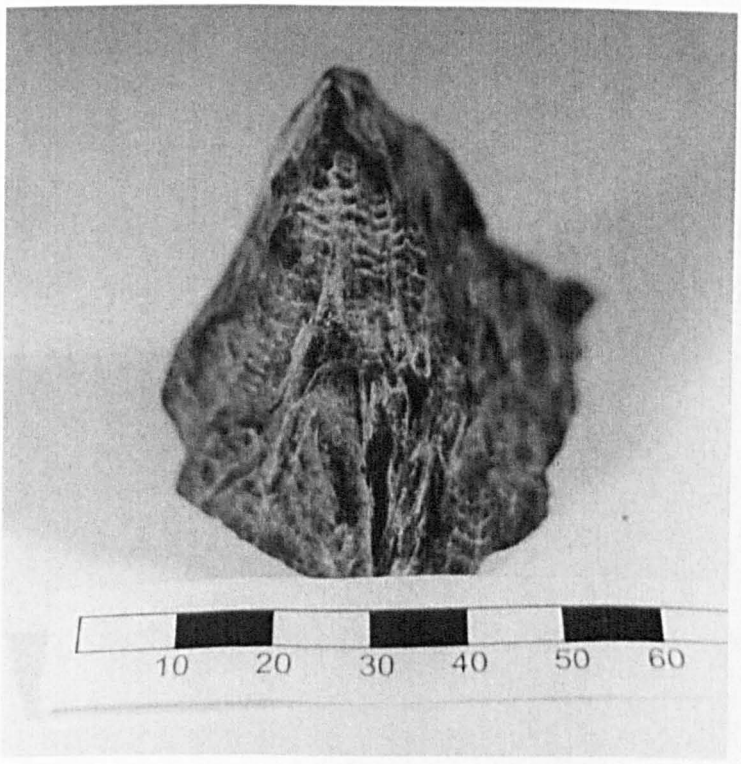


Figure 9.5a-c. Three views of the limestone gill raker block from the Atacama Desert, before CT scanning and destructive analysis. Scale bar = 60mm.

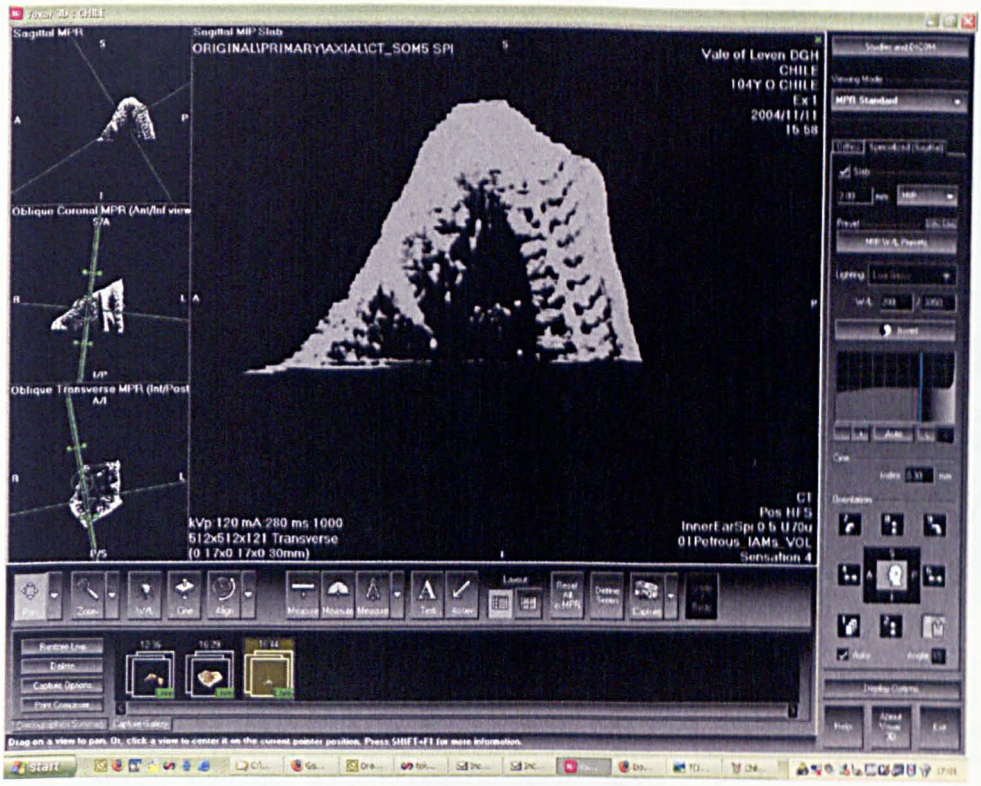


Figure 9.6a. Initial CT data image. Image courtesy of BARCO N.V.

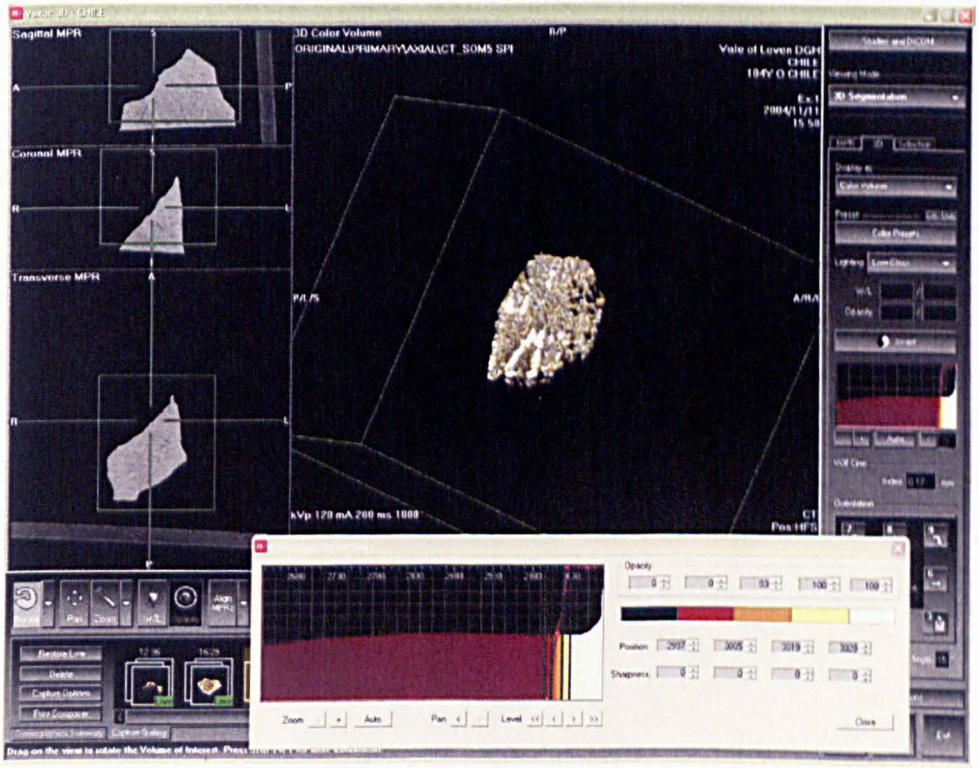


Figure 9.6b. Voxar 3D colour volume reconstruction showing longitudinal view down cavity of the gill raker stalk, with extensive internal resorption. Image courtesy of BARCO N.V.

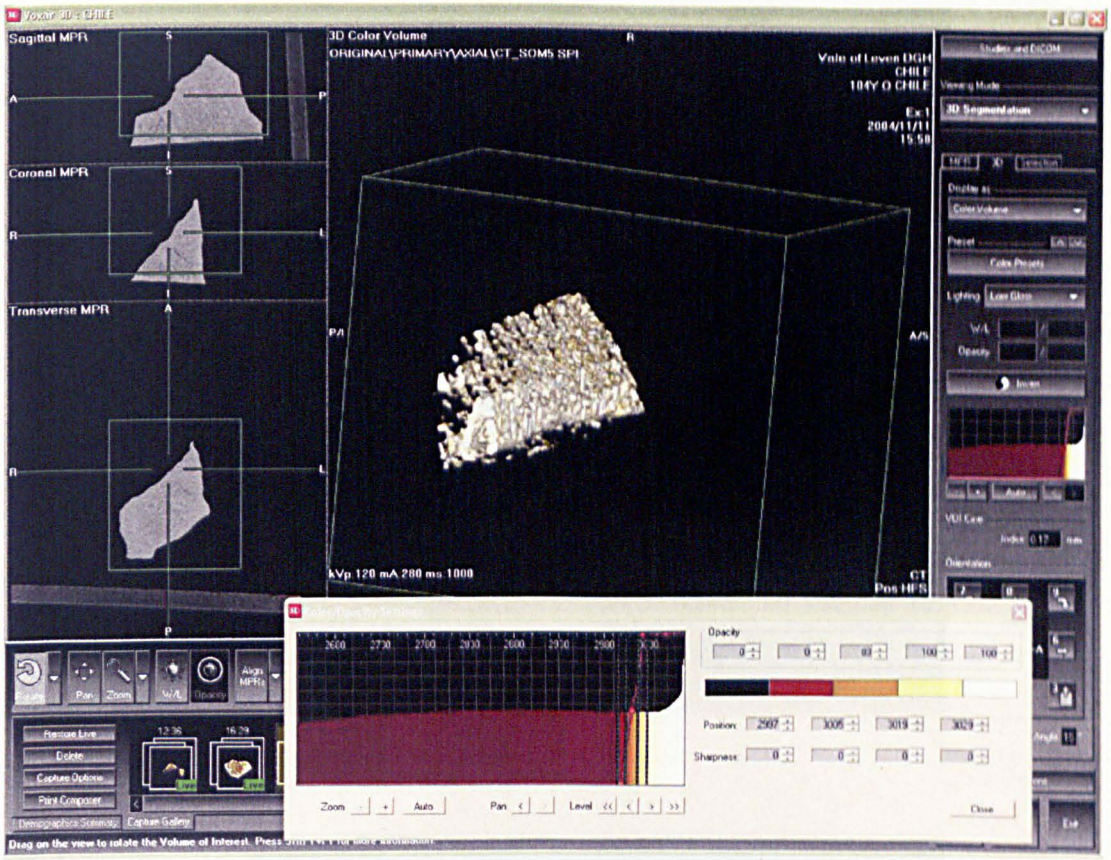


Figure 9.6c. Voxar 3D colour volume reconstruction showing oblique ridges of gill rakers in lateral view. Image courtesy of BARCO N.V.

Figure 9.6d. Cut surface of gill raker block. Block is 55mm across.

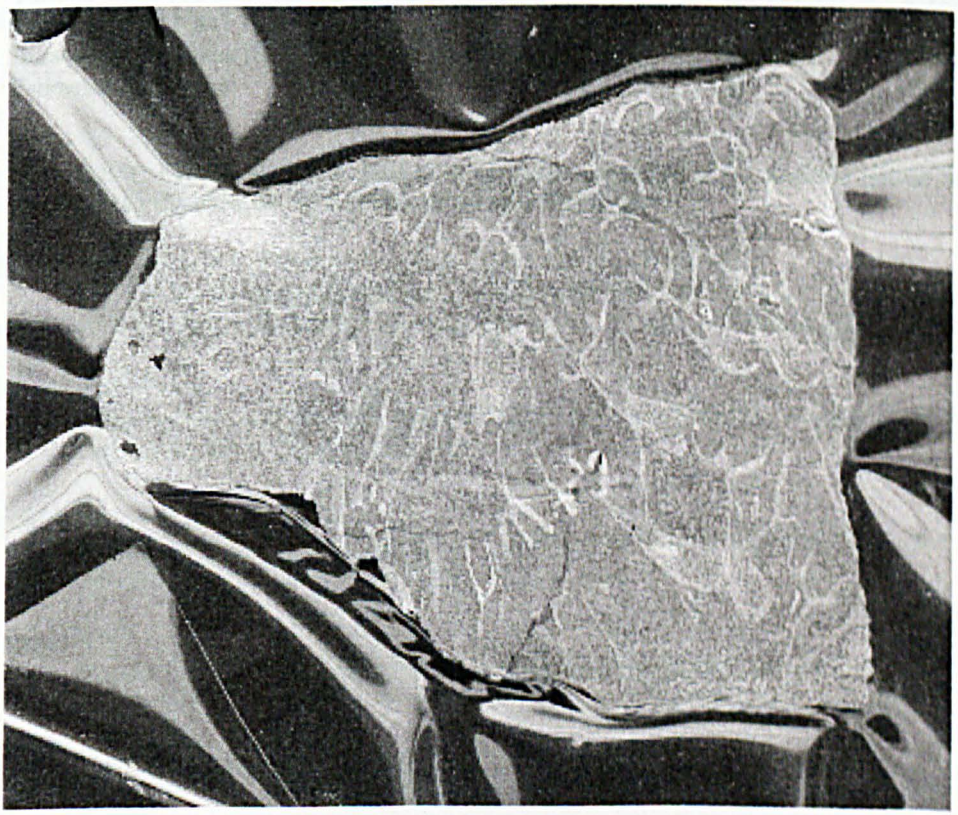


Figure 9.6e. Acetate peel from gill raker block. Peeled area of block is 55mm across.

Chapter 9: Tables

	Model	Scales to	Bainbridge prediction	Percentage Difference
Length (mm)	340	8913	N/A	N/A
Volume	408041.89mm^3	7322 litres	7080 litres	3.31%
Surface Area (mm^2)	50388.01	31692544.576	31776627.6	0.265%

Table 9.1. Comparison of volume and surface area of model and figures derived using Bainbridge (1961)

PARAMETER	Ariston	BMNH P.10000	Big Meg
Body Mass (tonnes)	5.208828813	7.080627045	18.81366
Surface Area (metres squared)	25.8952464	31.7766276	60.95961
Standard Length (metres)	8.046	8.913	12.345
Cruising muscle mass (tonnes)	0.13022072	0.177015676	0.470341
Sprint muscle mass (tonnes)	2.604414407	3.540313522	9.40683
Total muscle mass (tonnes)	2.734635127	3.717329199	9.877171
Steady swimming speed (ms-1)	1.6092	1.7826	2.469
Unsteady swimming speed (ms-1)	4.023	4.4565	6.1725
Approximation of Metabolic rate (Kleiber's Rule)	3.447903192	4.340640214	9.033477
Turning radius (constant fraction of length) in metres	1.36782	1.51521	2.09865
Cruising Speed (Gray 1968) (ms-1)	32.184	35.652	49.38
Burst speed (turbulent flow - Bainbridge 1961) (ms-1)	8.47ms-1	8.82ms-1	10.01ms-1
Estimated Age (years)	21	25	29

Table 9.2. Theoretical biological characteristics of three specimens of *Leedsichthys* derived from estimated lengths using equations of Webb (1975) unless otherwise noted.

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